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The effect of fires at different times of the year on vegetative and sexual reproduction of grasses, and on establishment of seedlings

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by

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INTRODUCTION

Fires have been common in grassland communities. Whereas grasslands do not record the frequencies of fires within themselves, surrounding woodlands can give some estimate of fire frequency. Using tree ring data, Bragg (1985) reported that fire frequencies were about 3.5 years in the oak/pine bluff forest of northcentral Nebraska prior to settlement by non-Indians. Arno and Gruell (1983) in southwestern Montana, and Abrams (1985) in northeastern Kansas, found less frequent fire scars, but estimated that the surrounding grassland regions burned more frequently. There can be little doubt that fires were a common event in North American grasslands.

Fire is used today as a tool for maintenance and management of prairie remnants. Most management practices involve burning in the spring. However, historical evidence indicates that fires occurred at any time of the year. They were started most frequently by lightning and man.

Lightning in the Midwest is most common in storms along fronts that sweep the broad plains, or accompanying convection storms (Komarek, 1966). Lightning fires have occurred between July and September in Saskatchewan (Rowe, 1969), and most frequently in July and August in the Dakotas and Montana (Higgins, 1984), Wyoming (Komarek, 1964), and Nebraska (Westover, 1977). Thunderstorm activity in Iowa is most common in late spring and throughout the summer.

For thousands of years, humans have used fire to enhance their survival (Komarek, 1967; Pyne, 1986), and the Great Plains has been no exception to this process. Pyne (1982) suggests that with the advent of man's influence, the number of spring or fall fires in the Great Plains increased. Indians burned grasslands for military and security reasons, and agricultural and hunting purposes, and these fires occurred at any time of the year (Moore, 1972; Nader, 1971; Pyne, 1982, 1986). In Iowa, historical fires occurred most frequently in summer and fall (Lyon, 1940; Moore, 1972). Only 25% of Indian caused fires occurred in the spring in Iowa (Moore, 1972). Present day accounts of wildfires in Iowa indicate that fires occur throughout the year, with peak frequencies in April and May (R. G. Hatcher, Iowa Conservation Commission, personal communication).

Prairies are susceptible to fires at any time of the year, because plant matter dries rapidly (Bragg, 1982a). Bragg (1982b) found that grassland flammability changed throughout the growing season. Tall grass prairie was least flammable in June, but flammability rapidly increased in July and August. Nevertheless, the area he studied was able to burn throughout the year. Steuter (1986) found that the rate of fire spread in a mixed prairie was least in the summer; however, he burned at average wind speeds. If a prairie fire were to start by a lightning strike accompanying a storm, higher than average wind speeds would probably occur, increasing the rate of fire spread.

Fires at various times of the year could affect the prairie community differently. The interplay of fires with the phenology of prairie plants would be expected to result in changes in plant community composition. Cool and warm season grasses are obvious components of prairies which, because of their phenological differences, may show contrasting responses to fires at different times of the year. Through study of prairie plant reproduction and seedling establishment, the long term effects of fires at different times of the year can be understood.

Some studies have looked at the effects of fires at times other than spring, especially fall or winter fires (Aikman, 1955; Anderson and Van Valkenburg, 1977; Bailey and Anderson, 1978; Burton, 1944; Curtis and Partch, 1948; Ehrenreich and Aikman, 1963; Henderson et al. 1983; Huffman and Kapustka, 1984; James, 1985; Kline, 1986; Lovell et al. 1983; McMurphy and Anderson, 1965; Owensby and Lauchbaugh, 1977; Schacht and Stubbendieck, 1985; Towne and Owensby, 1984; White and Currie, 1983; Young and Evans, 1978), but few studies have incorporated summer burns (but see Adams et al. 1982; Biswell and Lemon, 1943; Steuter, 1986; Trlica and Schuster, 1969). Hover and Bragg (1981) compared spring and summer mowing to spring fire in an attempt to study summer disturbances that resemble burning and their effect on grasses.

Most studies, including those above, and those reviewed by Daubenmire (1968), Hulbert (1986), Risser et al. (1981), Vogl (1974), and Wright and Bailey (1980, 1982), have looked at fires and their effect on phytomass, cover, or flowering. Flowering can give some indication of changes in potential seed input resulting from the fire. Unfortunately, biomass does not give informative details of vegetative reproduction of plants. Rarely have prairie fire studies looked at vegetative reproduction or seedling establishment.

I have concentrated on tillering (vegetative reproduction), flowering, and seed production of Andropogon gerardii and Sorghastrum nutans (warm season grasses), and Poa pratensis (a cool season grass), to ascertain the effects of timing of fires on reproduction of species with different phenologies. I have also investigated seedling establishment of all species to find how the timing of burns affects recruitment into a prairie community.

METHODS

Study Site

The study was conducted in a private prairie on a northeast facing shoulder slope above Indian Creek, T84N R23W, Sec. 25, Story County, Iowa. The land was purchased by the current owner in the 1950s and had been grazed in the fall until the mid 1960s. Since that time, it has remained idle. The prairie was burned (as a management tool) in the spring of 1983. The area is dominated by Andropogon gerardii, Sorghastrum nutans, and Poa pratensis. Other important species include Panicum scribnerianum, Stipa spartea, Andropogon scoparius, Amorpha canescens, Rosa spp., Viola pedatifida, Pastinaca sativa, and Daucus carota. A complete list of species found in the prairie is presented in Appendix A. Voucher specimens of plants within the prairie were collected and are stored in ISC (Iowa State Herbarium Collection). Nomenclature of grasses is from Pohl (1966), of sedges from Gilly (1946), and of all other species from Gleason and Cronquist (1963).

Design

The experiment was conducted using a randomized complete block design with seven replications. The slope, direction, and soil characteristics of each block are given in Appendix B. Each block contained eight .5 m X 2 m plots arranged in two rows of four plots each. Each plot had a 25 cm buffer all around, to avoid edge effects. The plots were separated from nearby plots by 1 m strips. The plots in each block were randomly assigned to a burn time, and one plot in each block was left unburned.

The burns were conducted in 1985 on 18 May, 29 June, 20 August, and 3 November, and in 1986 on 6 May, 17 July, and 19 August. The time of the burns in relation to flowering of prairie plants is given in Appendix C. Before each fire, fire breaks were created by clipping and raking strips around the treatment plots and their buffers. An aluminum flashing surrounded the burn area (including the buffer area) to help control the fire. The burns were conducted when the thatch was dry, or nearly so, and at low wind velocity. Most plots burned completely, leaving only ash and a few woody or stout (but dead) stems. In a few plots of the November burn, some small patches of litter remained. In the August 1986 burns, flowering stalks of *Andropogon gerardii* and *Sorghastrum nutans* were burned off at the ground but were not fully consumed by the fire.

Data Collection and Analyses

Statistical differences were determined at $p \leq 0.05$ overall level of significance. Conservative comparisons of means were made on all parametric analyses using Bonferoni alpha levels. Comparisons of rank totals of nonparametric tests were made at the $p \leq 0.05$ overall level of significance. Due to spatial heterogeneity of grass distribution, not all species were represented in each plot. Therefore, population parameters were estimated in most parametric analyses as least-squares means and standard errors (Cochran and Cox, 1957).

Environmental data

Soil temperature Surface soil temperature was measured by inserting a soil thermometer 2 cm into the soil at the border of each plot.

Measurements were taken on burned plots and nonburn plots during high lights hours. All measurements in a day were taken within two hours of each other. Measurements were taken in 1985 on 3 and 28 June, 23 July, 9 August, and 15 October, and in 1986 on 2 and 23 July.

Soil moisture Soil moisture was determined in two cores, 4.5 cm deep, 2 cm in diameter, which were removed from the border of each plot and mixed. The samples were put in metal cans which were capped and transported to the lab. The roots were removed from the samples. Samples were weighed, dried at 60^{0}C for four days, and weighed again. Per cent moisture was determined on a dry weight basis. Samples were taken in 1985 on 10 and 28 June, 23 July, 9 August, and 17 October, and in 1986 on 23 July and 2 September. Soil samples were not taken during May or June of 1986 because of frequent and substantial rainfall; differences in soil moisture between treatments would have been unlikely.

Light measurements The amount of light between 400 and 700 nm was measured at ground level using a Licor 190S quantum sensor. All light measurements were taken within one or two hours of solar noon. On 3 and 28 June, 23 July, 8 August, and 15 October 1985 and on 2 July 1986, a single measurement per plot was taken at a consistent position in each plot. On 31 July and 8 September 1986, five measurements were taken per plot, at equally spaced intervals. At the same time, a second quantum sensor measured direct sunlight. These last two sets of data were converted to per cent incident light at ground level.

All environmental data were analyzed using analysis of variance.

Tillering

The tillers of *Andropogon gerardii*, *Sorghastrum nutans*, and *Poa pratensis* were counted in permanent 50 cm X 50 cm areas within the plots. Tillers were counted for plots of unburned, June, and August 1985 burns between 25 June and 3 July 1985. All plots, 1985 and 1986 treatments, were counted between 6-16 September 1985, between 23 May and 18 June 1986, and between 18 August and 6 September 1986.

The tiller counts were analyzed by analysis of covariance using the pretreatment counts (25 June-3 July, or 6-16 September 1985) as the covariate. Preburn spring counts for 1986 contained only a few warm-season grass tillers at a stage prior to leaf expansion, making identification difficult. Therefore, preburn spring counts were an unreliable measure of warm season grass tillers. Fall 1985 counts, then, were better indicators of the amount of tillers present before 1986 burns.

Flowering culms

Flowering culms of *A. gerardii*, *S. nutans*, and *P. pratensis* were counted in each plot. *P. pratensis* was counted and calculated on a 1 m^2 basis. *A. gerardii* and *S. nutans* were counted and calculated by the basal area of clumps or clones of each species in each plot. *P. pratensis* was counted in June 1985 and between 19 May and 10 June in 1986. *A. gerardii* and *S. nutans* were counted between 20-26 September 1985, and 13-26 September 1986.

P. pratensis was analyzed with analysis of variance, using transformed data: $\ln(\text{flowering culms}/m^2 + 1)$. *A. gerardii* and *S. nutans* were analyzed by analysis of covariance of $\ln(\text{flowering culms}/m^2 + 1)$, using ln(basal area ($m^2$)) as the covariate; this was the best linear relationship between flowering culms and basal area.

Seed production

Five inflorescences of each of the three species were harvested in each plot. If fewer than five inflorescences were present, all were harvested. The inflorescences were harvested by systematically selecting the closest inflorescence to each center of five equal subdivisions of the plot. The inflorescences were clipped, packaged separately, labelled, and oven dried at 60^0C for two to three days.

A. gerardii and *S. nutans* were harvested on 17-18 September 1985 for May 1985 burn plots and for nonburn plots, and on 1 October 1985 for plots burned in June 1985. Harvesting of the same species occurred on 27 September 1986 for all plots but those burned in July 1986, which were harvested on 8 October 1986. No *P. pratensis* was harvested in 1985, because there were almost no flowering culms. In 1986, they were harvested on 10 June.

The developed caryopses of each inflorescence were counted. Analysis of variance was conducted on the data, using the mean square error from plot means to determine block and treatment effects.

Seedlings

Seedlings were marked in each plot using wooden golf tees. The tees were color coded to distinguish warm-season grasses, *P. pratensis*, *Panicum scribnerianum*, and dicots. The seedlings were marked throughout the growing season: in 1985 on 5 June, 10 and 22-30 July, 5-21 August, and 4-12

October, and in 1986 on 19 May-16 June, 9-30 July, and 7 September-4 October. In 1985, seedlings were marked throughout the entire plot. In 1986, due to a high number of seedlings, monocots were marked in full plots and dicots were marked in half plots. During 1985, the appropriate tee was removed upon the death of a seedling. Species composition of seedlings marked in 1985 was recorded on 17 June 1986 and between 13 September and 4 October 1986. Species of seedlings marked in 1986 were identified between 13 September and 4 October 1986.

The seedlings were analyzed using the nonparametric Freidman test on 6 blocks; two plots in block G had sustained pocket gopher damage. The seedlings were categorized into the following divisions: monocot/dicot, annual/biennial/perennial, and native/nonnative species. The nonparametric sign test was used to compare groups within treatments. The Freidman test was used to compare separately each division between treatments.

RESULTS AND DISCUSSION

Environmental Conditions

Rainfall

Monthly rainfall, recorded near Ames in Story County, Iowa, along with the 30 year average between 1951-1980, was compiled from the Climatological Data Bulletin (Fig. 1). Rainfall was below the 1951-1980 average during the 1985 growing season. Seven months of the year had below average rainfall, mainly during the growing season. May, being the month of greatest departure, was 7.9 cm below average. April and July were at least 5 cm below average. Rainfall was above average between August and October.

Rainfall was above average in 1986. During the growing season, only August had below average rainfall. July, September, and October each had rainfall at least 5 cm above average.

Effect of fires on soil and light conditions

Soil temperature Soil temperatures increased after burning. During the growing season of 1985, soil temperatures were 5-8^{0}C higher in plots burned in May than unburned plots (Fig. 2). In July and August, soil temperatures in June burn plots were 11-13^{0}C higher than unburned plots. Plots burned in August 1985 had significantly higher soil temperatures even in July 1986. In July 1986, May 1986 burn plots were 3^{0}C higher than unburned plots (Fig. 3). After the burning, July burn plots were 5^{0}C higher than unburned plots.

Soil moisture Within two to three weeks after burns, soil moisture was higher in burned plots than unburned plots (Fig. 4). Four or

Figure 1. Monthly rainfall near Ames, Iowa, compiled from the <u>Climatological Data Bulletin</u> (●-1951-1980 average, ○-1985, △-1986)

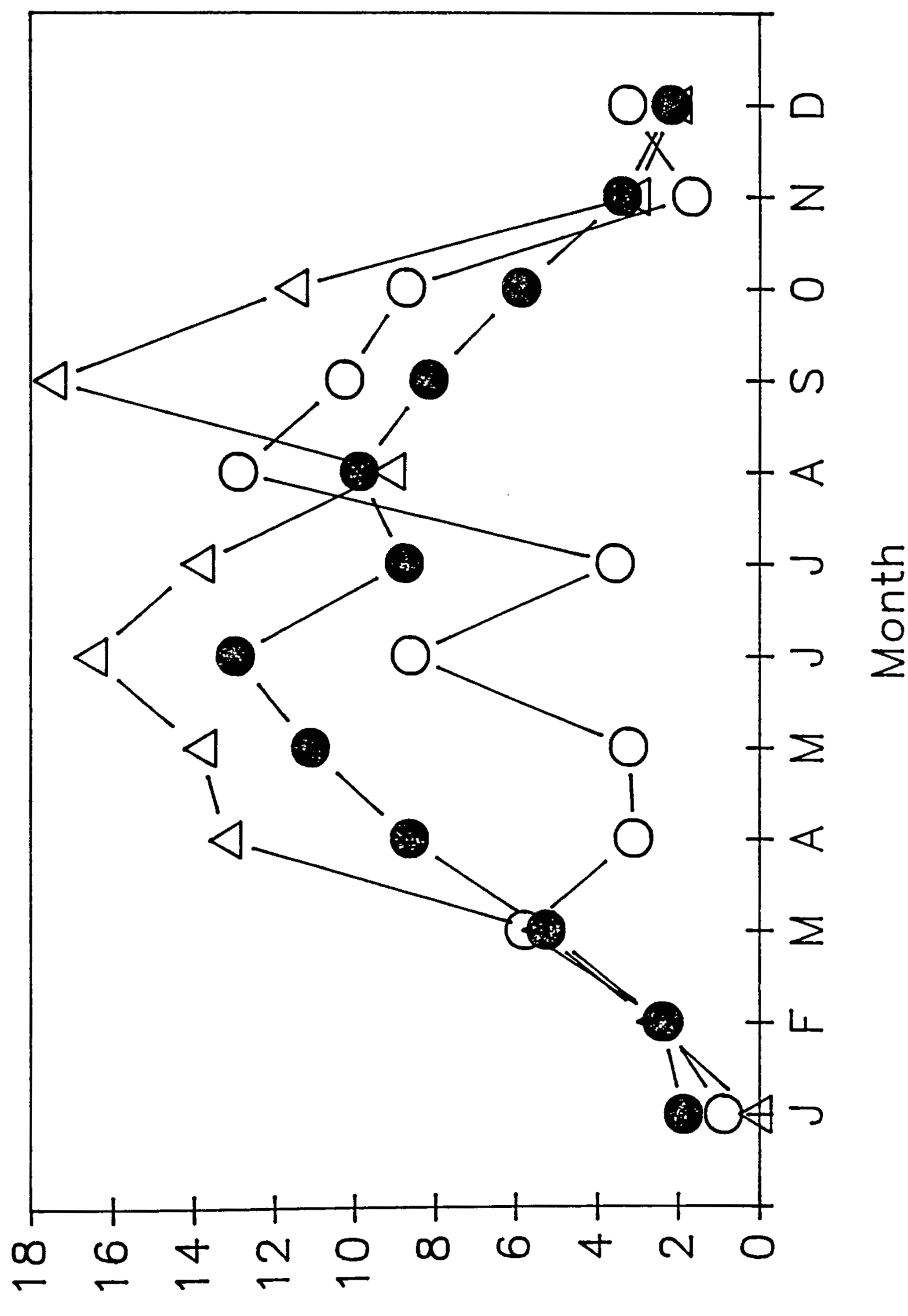
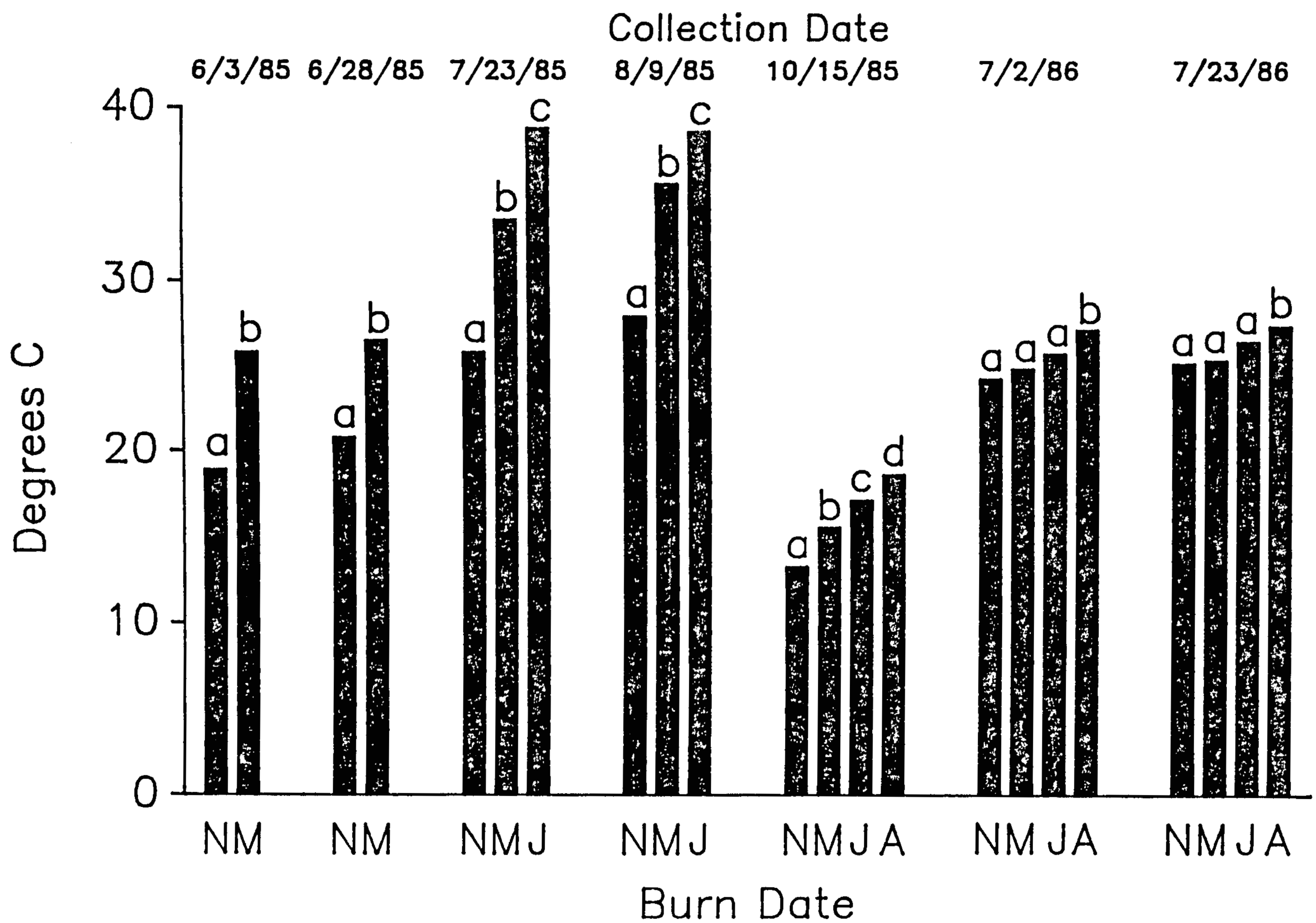

Rainfall (cm)
0
2
4
6
8
10
12
14
16
18
J
F
M
A
M
J
J
A
S
0
N
D
Month

Figure 2. Soil temperature of plots burned in 1985 (N=No burn, M=May burn, J=June burn, A=August burn, different letters above columns within a set indicate statistically different means)



Collection Date
6/3/85
6/28/85
7/23/85
8/9/85
10/15/85
7/2/86
7/23/86
Degrees C
40
30
20
10
0
a
b
a
b
a
b
c
a
b
c
a
b
c
d
a
a
a
b
a
a
a
b
NM
NM
NMJ
NMJ
NMJA
NMJA
NMJA
Burn Date

Figure 3. Soil temperature of plots burned in November 1985 or during 1986 (NB=No burn, N=November burn, M=May burn, J=17 July burn, different letters above columns within a set indicate statistically different means)

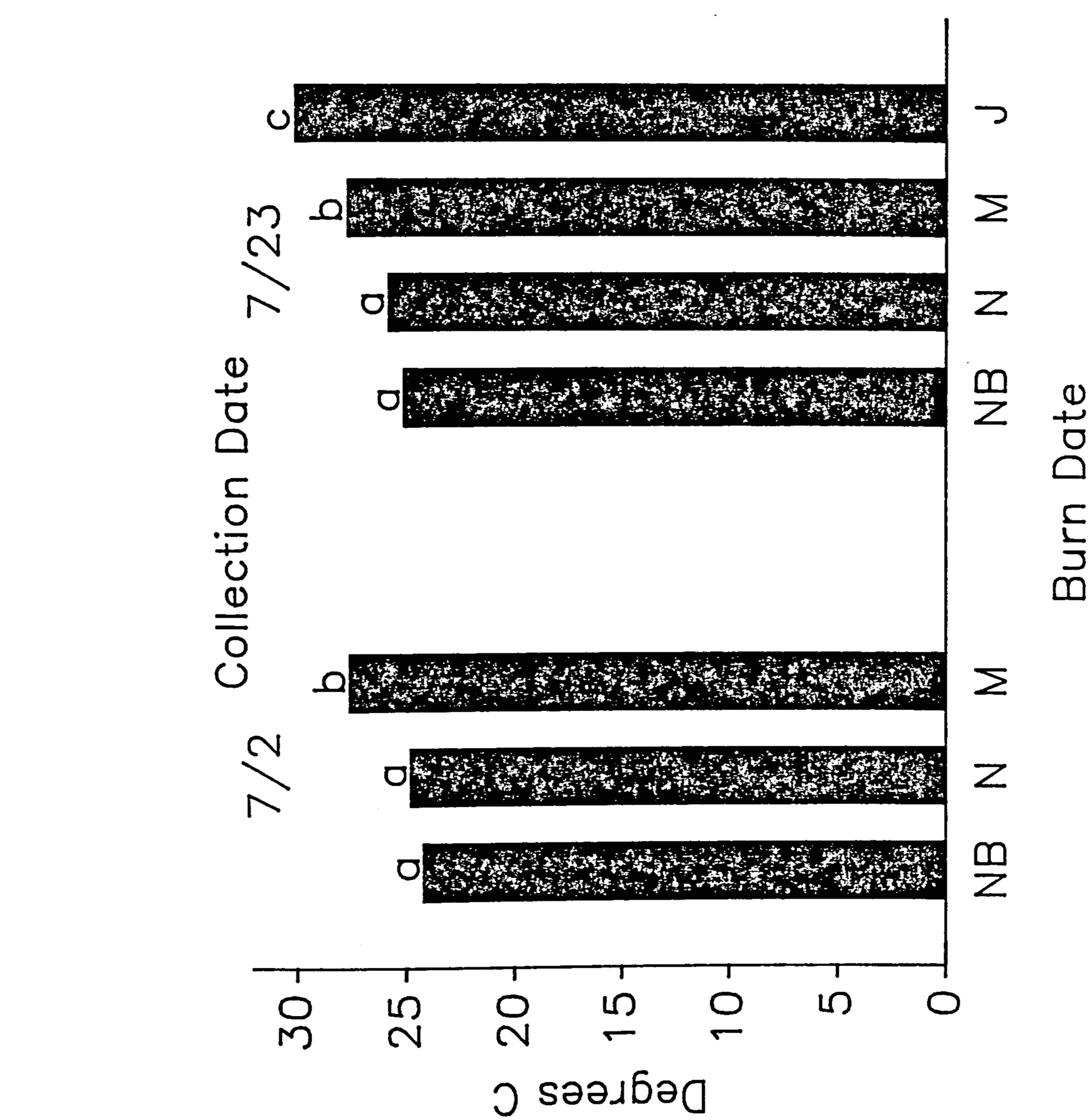
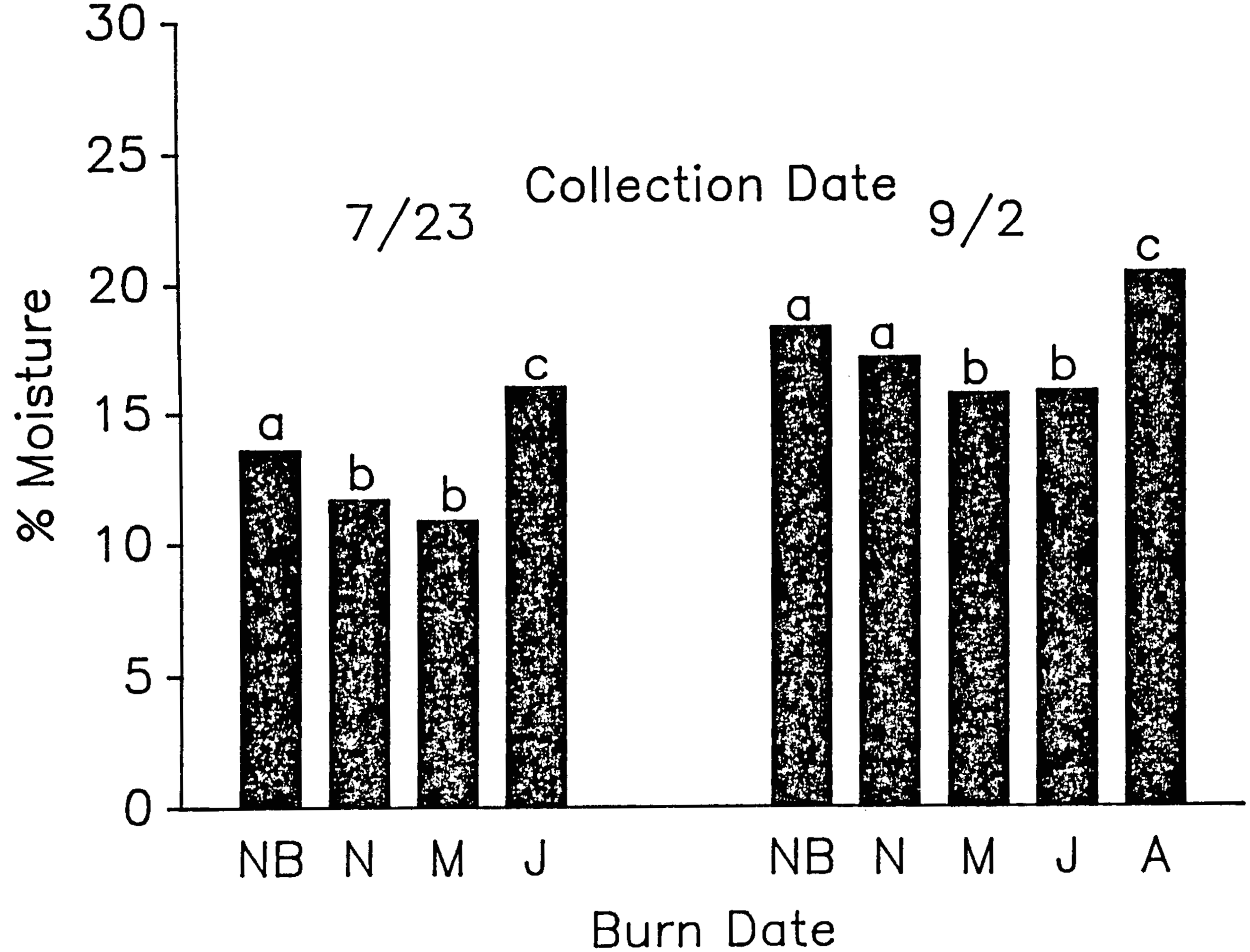

Collection Date
7/2
7/23
a
a
b
a
a
b
c
30
25
20
15
10
5
0
Degrees C
NB
N
M
NB
N
M
J
Burn Date

Figure 4. Soil moisture in plots burned in November 1985 or during 1986 (NB=No burn, N=November burn, M=May burn, J=July burn, different letters above columns within a set indicate statistically different means)


Collection Date
7/23
9/2
% Moisture
0
5
10
15
20
25
30
a
b
b
c
a
a
b
b
c
NB
N
M
J
NB
N
M
J
A
Burn Date

five weeks after burns, soil moisture was significantly lower in burned plots than unburned plots (Fig. 5). The trend of lower soil moisture in burned plots continued into the second growing season (Figs. 4, 5).

Light measurements Light measurements were much greater at ground level following burning (Figs. 6, 7, 8). The 1985 burn plots, with the exception of the May burn, received more light at ground level than unburned plots, until at least July of the following year (Fig. 7). Increased growth of tillers and flowering of grasses decreased ground level light in May and November burn plots (Figs. 6, 8).

Vegetative Responses

Tillering

Warm season grasses Little regrowth of *A. gerardii* occurred in the month following August burns. Consequently, in 1985, August burn plots, when counted in September 1985, had significantly fewer tillers than June burn plots but not significantly fewer than unburned plots (Fig. 9a). Also, in 1986, August burn plots had significantly fewer tillers than Nov. 1985 and May 1986 burn plots (Fig. 9a). In June of the second growing season, August 1985 burn plots still had fewer tillers of *A. gerardii* than June 1985 burn plots (Fig. 9b). However, by August 1986, tiller counts were similar among treatments.

In 1985, *S. nutans* had similar tiller counts (i.e., no significant differences) between burned and unburned plots (Fig. 10a). This similarity continued in 1986 (Fig. 10b). In 1986, Nov. 1985 burn plots had significantly higher tiller counts of *S. nutans* than August 1986 burn plots (Fig. 10a).

Figure 5. Soil moisture in plots burned in 1985 (N=No burn, M=May burn, J=June burn, A=August burn, different letters above columns within a set indicate statistically different means)

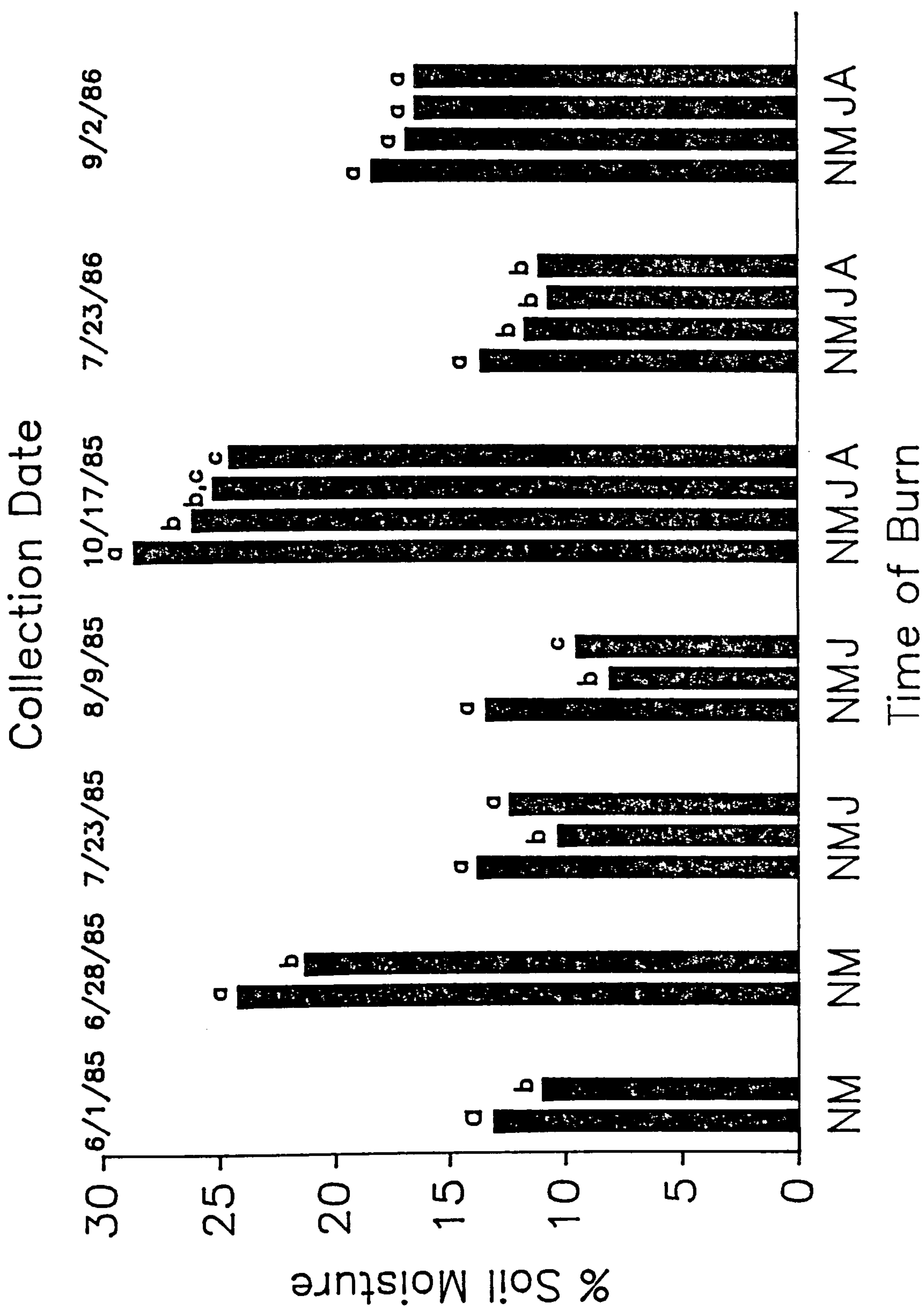

Collection Date
6/1/85
6/28/85
7/23/85
8/9/85
10/17/85
7/23/86
9/2/86
% Soil Moisture
0
5
10
15
20
25
30
Time of Burn
NM
NM
NMJ
NMJ
NMJA
NMJA
NMJA
a
b
b,c
c

Figure 6. Photosynthetic Photon Flux Density (PPFD) (μmol $m^{-2}sec^{-1}$) between 400-700 nm measured at ground level in plots burned in 1985 (N=No burn, M=May burn, J=June burn, A=August burn, different letters above columns within a set indicate statistically different means)

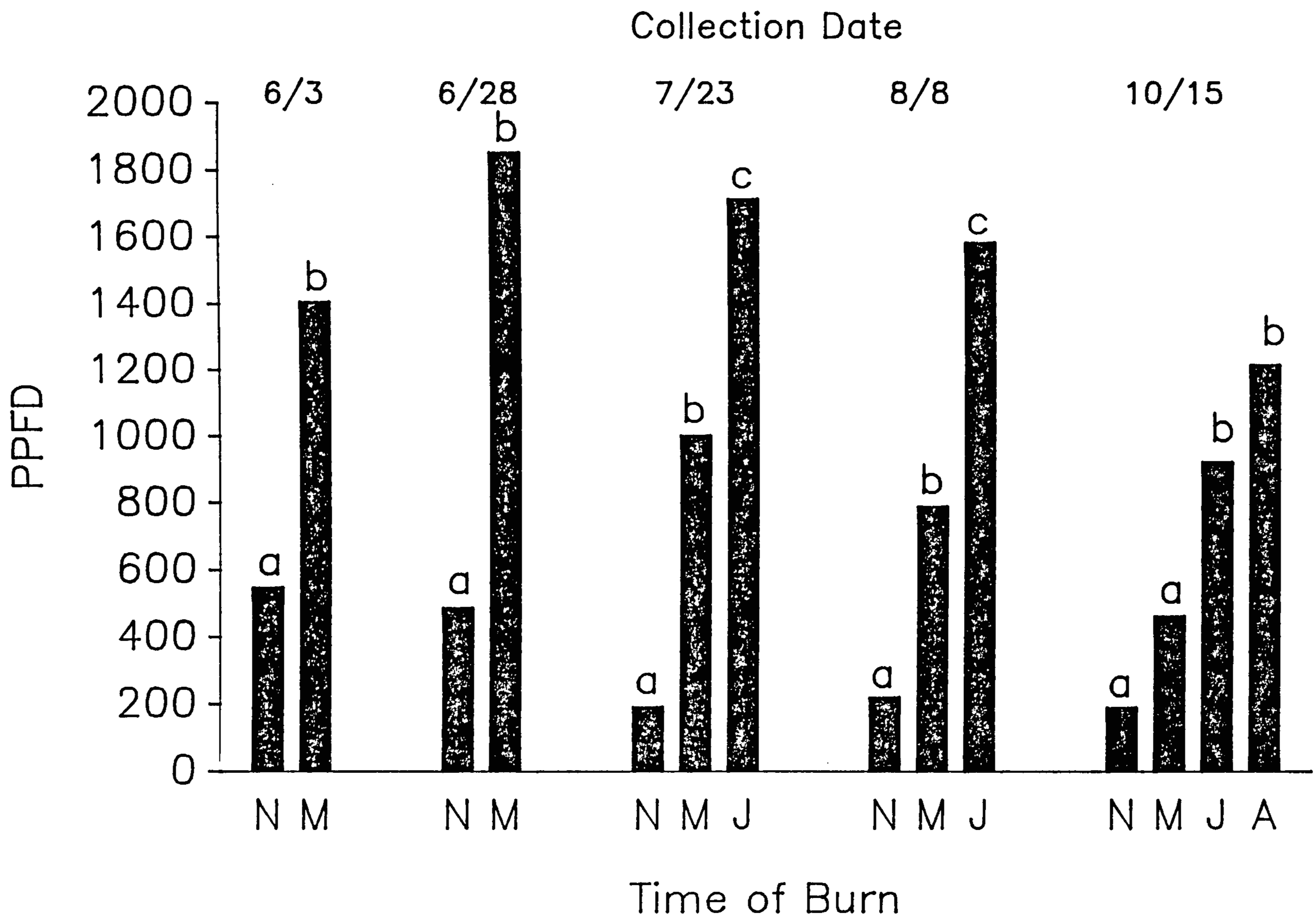

Collection Date
6/3
6/28
7/23
8/8
10/15
PPFD
2000
1800
1600
1400
1200
1000
800
600
400
200
0
a
b
a
b
a
b
c
a
b
c
a
a
b
b
N M
N M
N M J
N M J
N M J A
Time of Burn

Figure 7. Light measurements at ground level measured in 1986 on 1985 burn plots (PPFD=Photosynthetic photon flux density (μmol $m^{-2}sec^{-1}$) between 400-700 nm, NB=No burn, M=May burn, J=June burn, A=August burn, different letters above column within a set indicate statistically different means)

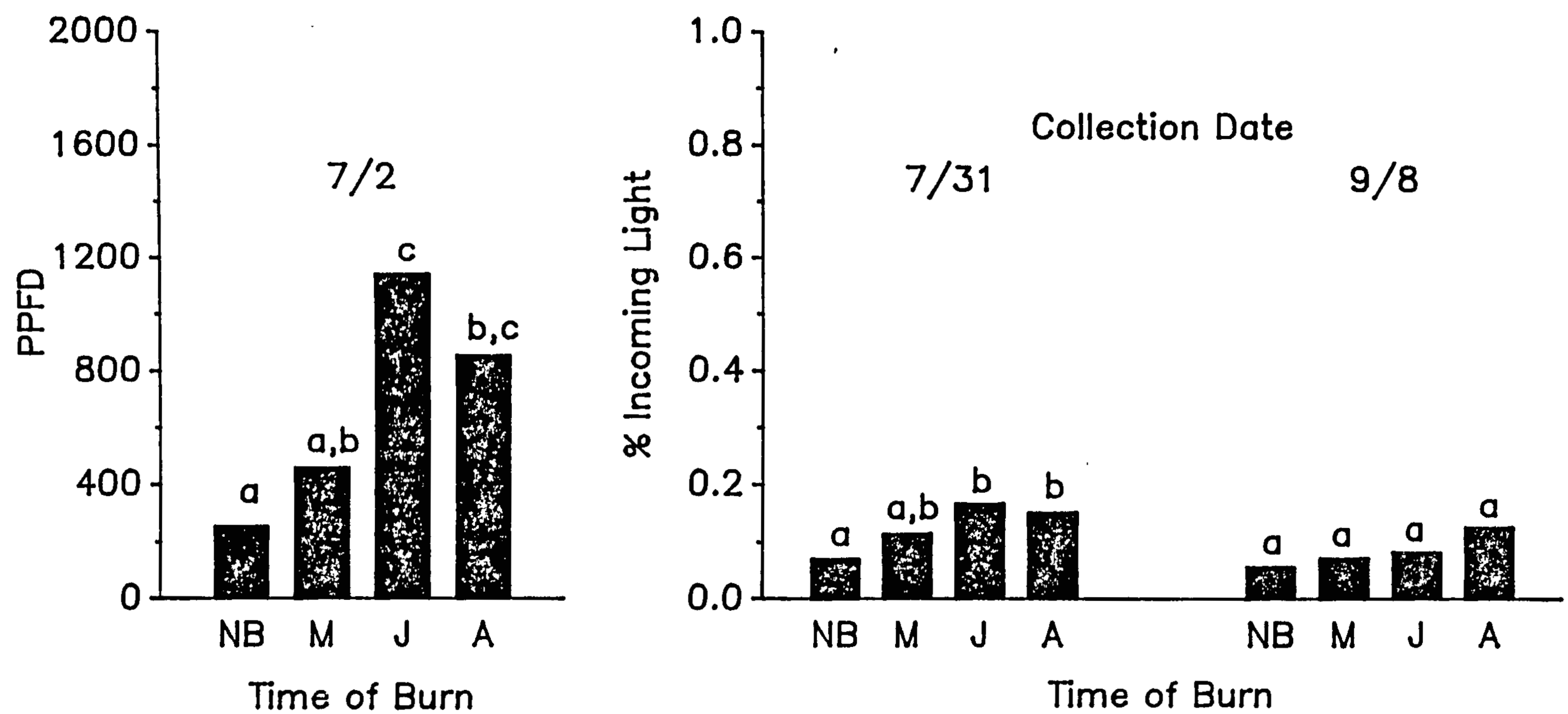
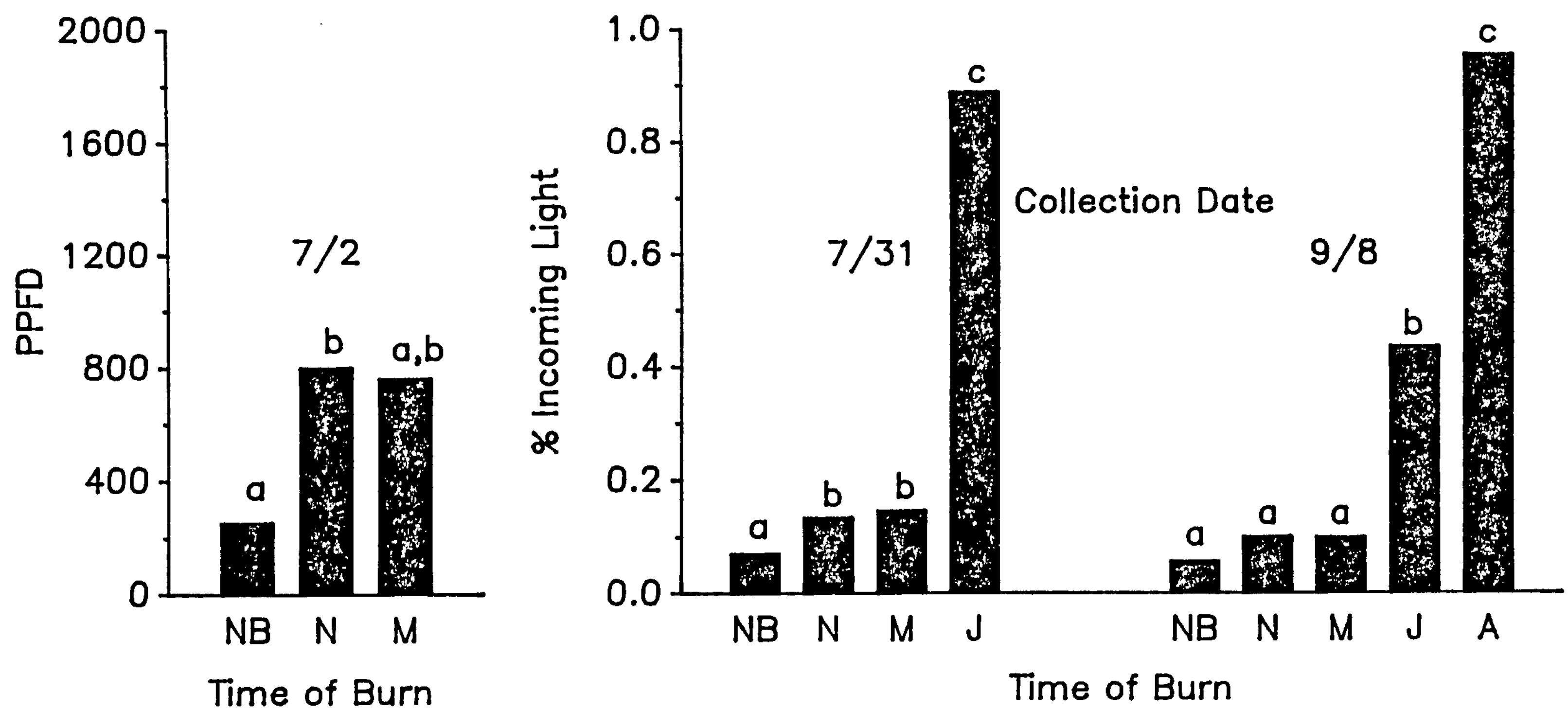

PPFD
2000
1600
1200
800
400
0
7/2
a
a,b
c
b,c
NB M J A
Time of Burn
% Incoming Light
1.0
0.8
0.6
0.4
0.2
0.0
Collection Date
7/31
9/8
a
a,b
b
b
a
a
a
a
NB M J A NB M J A
Time of Burn

Figure 8. Light measurements at ground level measured in 1986 on plots burned in November 1985 and during 1986 (PPFD=Photosynthetic photon flux density (μmol $m^{-2}sec^{-1}$) between 400-700 nm, NB=No burn, M=May burn, J=July burn, A=August burn, different letters above column within a set indicate statistically different means)



PPFD
2000
1600
1200
800
400
0
7/2
a
b
a,b
NB
N
M
Time of Burn
% Incoming Light
1.0
0.8
0.6
0.4
0.2
0.0
Collection Date
7/31
9/8
a
b
b
c
a
a
a
b
c
NB
N
M
J
NB
N
M
J
A
Time of Burn

Figure 9. The effect of burning on tillering of _Andropogon gerardii_: a. Tillering during first growing season after burns, b. Tillering during second growing season after burn (NB=No burn, JN5=June 1985 burn, AU5=August 1985 burn, NV5=November 1985 burn, MY6=May 1986 burn, JL6=July 1986 burn, AU6=August 1986 burn, error bars on columns indicate one standard error from mean, different letters above columns within a set indicate statistically different means)

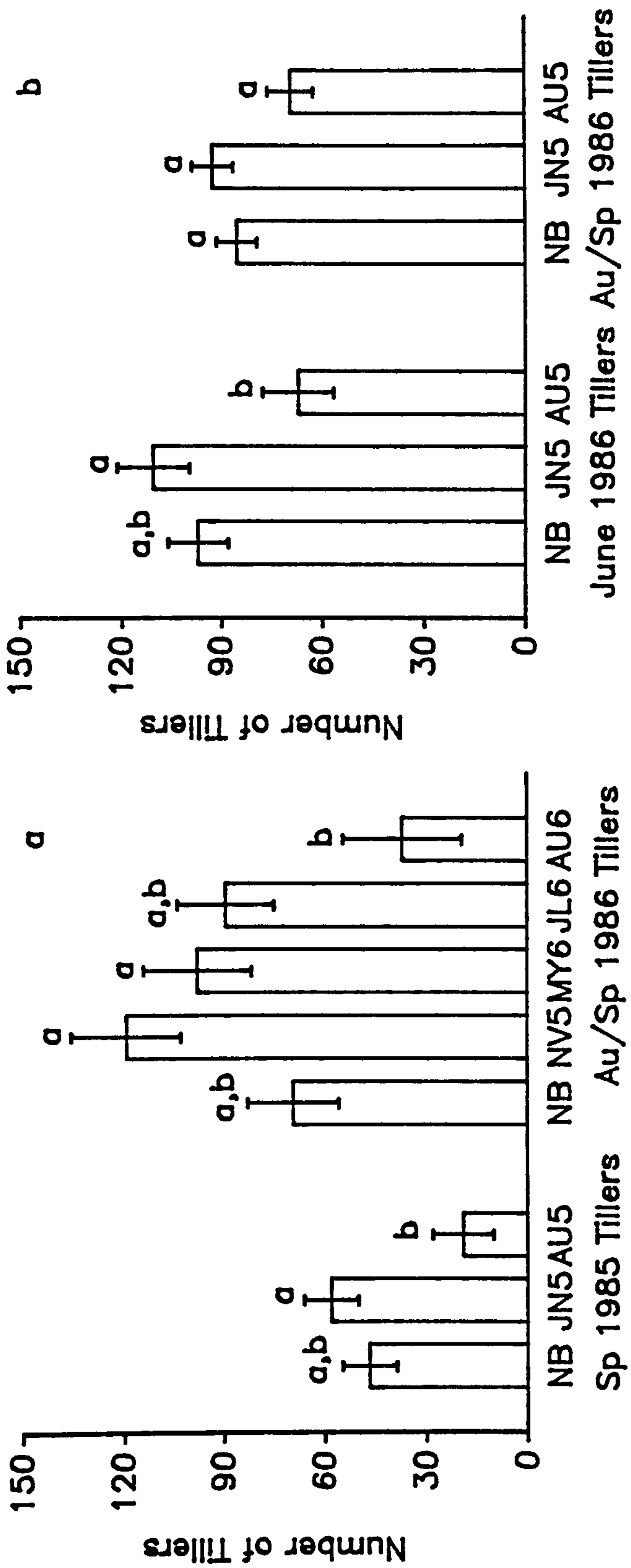
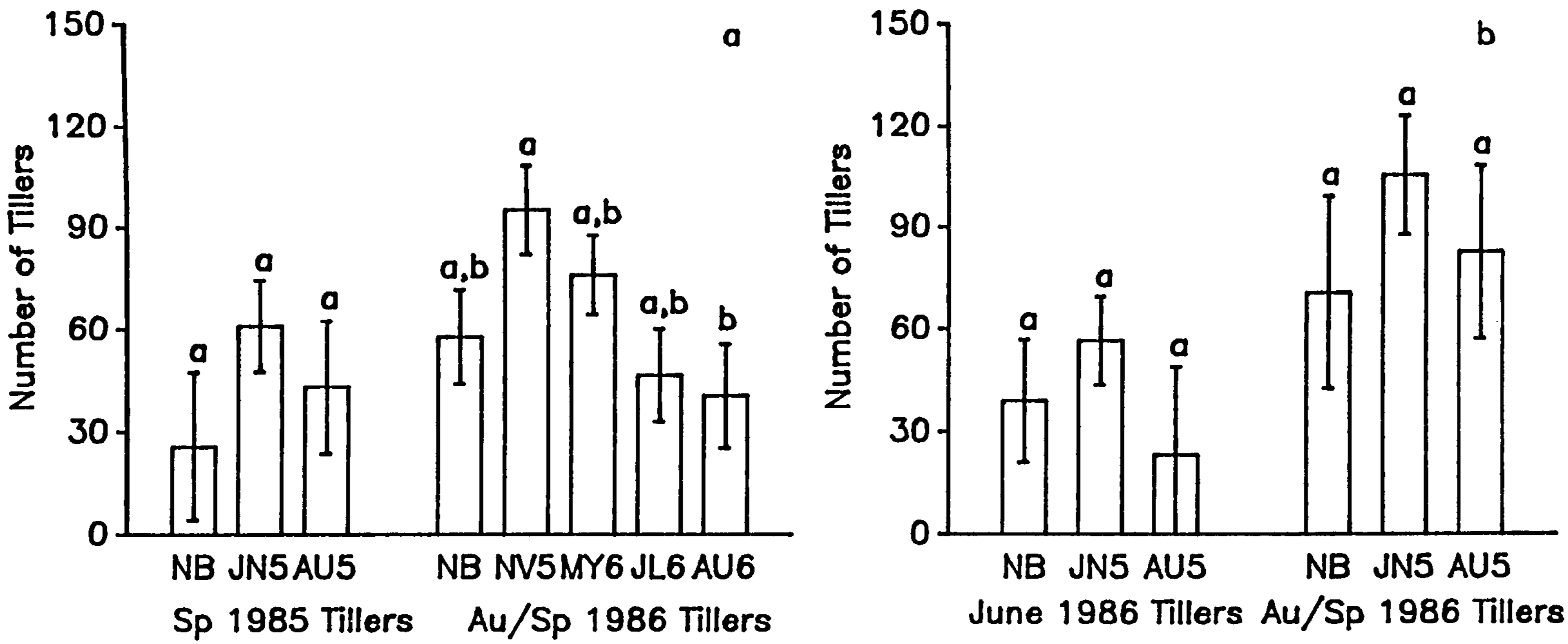

Number of Tillers
150
120
90
60
30
0
a,b
a
b
NB JN5 AU5
Sp 1985 Tillers
a,b
a
a
a,b
b
a
NB NV5 MY6 JL6 AU6
Au/Sp 1986 Tillers
Number of Tillers
150
120
90
60
30
0
a,b
a
b
NB JN5 AU5
June 1986 Tillers
a
a
a
b
NB JN5 AU5
Au/Sp 1986 Tillers

Figure 10. The effect of burning on tillering of _Sorghastrum nutans_: a. Tillering during first growing season after burn, b. Tillering during season growing season after burn (NB=No burn, JN5=June 1985 burn, AU5=August 1985 burn, NV5=November 1985 burn, MY6=May 1986 burn, JL6=July 1986 burn, AU6=August 1986 burn, error bars on columns indicate one standard error from mean, different letters above columns within a set indicate statistically different means)


150
120
90
60
30
0
Number of Tillers
a
a
a
a,b
a
a,b
a,b
b
a
NB JN5 AU5
Sp 1985 Tillers
NB NV5 MY6 JL6 AU6
Au/Sp 1986 Tillers
150
120
90
60
30
0
Number of Tillers
b
a
a
a
a
a
a
NB JN5 AU5
June 1986 Tillers
NB JN5 AU5
Au/Sp 1986 Tillers

In general, little regrowth of either A. gerardii or S. nutans occurred between August burns and September counts, resulting in distinctive treatment differences at that time. A. gerardii seemed to be more sensitive to the August burn than S. nutans, because tiller differences remained at the beginning of the second growing season for A. gerardii, but not for S. nutans. While treatment differences in tiller counts were significant between treatments, no burn treatment resulted in significantly higher or lower tiller counts than unburned plots for either A. gerardii or S. nutans. The differences noted between burn dates, therefore, indicate interactions of the fires with the seasonal growth patterns of the grasses. By the end of the second season, however, no differences between treatments remained. Thus, there were no long-term effects from burns at any time of the year on the vegetative reproduction of A. gerardii and S. nutans.

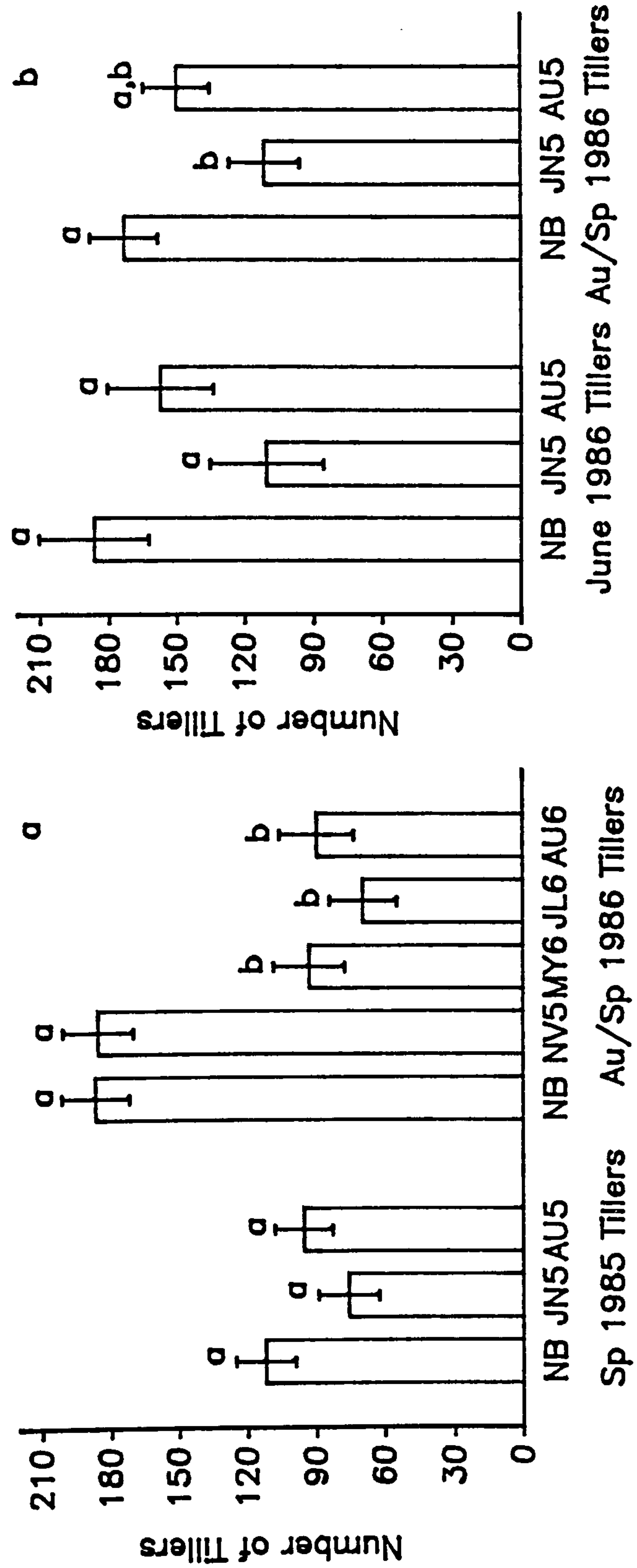
In one instance, A. gerardii had fewer tillers in a plot with deep soil burned in the spring of the previous year than a plot burned in the spring in the year of the count (Dokken and Hulbert, 1978). No differences were reported in plots located in shallow soil. The data in this study are, unfortunately, unreliable because of no replication. Two studies have reported increased tillering of warm season grasses following spring burns. Launchbaugh (1972) noted that Panicum virgatum, which had been planted in rows, produced twice as many tillers as plants in unburned rows. In this case, increased tillers may have been at least partially due to spaces between rows of grasses. Hulbert (1969), in a Kansas prairie which had not been burned for at least ten years, reported that A. gerardii produced two and a half times as many tillers following an April burn than in unburned areas. Although my results are suggestive of increased tillering of A. gerardii and S. nutans following a spring burn, no such pattern could be firmly established. The difference between their studies and mine could be due to different environmental conditions during the growing season, the number of years since a previous burn, or differences in the time of fire with respect to the phenology of the plants.

Poa pratensis In 1985, P. pratensis showed no differences in tillering among burned and unburned plots (Fig. 11a), but by August of 1986, unburned plots had significantly higher tiller counts than plots burned in June 1985 (Fig. 11b). Thus, there appears to be a second year effect on P. pratensis tiller formation. In 1986, fewer tillers of P. pratensis were present in spring and summer burn plots than fall and unburned plots (Fig. 11a).

The P. pratensis results probably show the influence of weather patterns on the impact of the burns. In 1985, the dry year, no difference was seen in tillering, but June 1985 burn plots did not establish as many new tillers as other plots in 1986, when the rainfall was substantial. Spring and summer burns also reduced tillers in the wet year, but not during the dry year.

Dokken and Hulbert (1978) reported that P. pratensis had fewer tillers in one plot with shallow soil that was burned in spring the previous year than a plot in shallow soil burned in that year. No differences were detected in deep soil. Unfortunately, the data from this study are unreliable because of no replication. Zedler and Loucks (1969) reported that spring burning in Wisconsin resulted in decreased or similar shoot density on burned ridges compared to unburned ridges, but increases

Figure 11. The effect of burning on tillering of _Poa pratensis_: a. Tillering during first growing season after burn, b. Tillering during second growing season after burn (NB=No burn, JN5=June 1985 burn, AU5=August 1985 burn, NV5=November 1985 burn, MY6=May 1986 burn, JL6=July 1986 burn, AU6=August 1986 burn, error bars on columns indicate one standard error from mean, different letters above columns within a set indicate statistically different means)


Number of Tillers
210
180
150
120
90
60
30
0
a
a
a
a
b
a,b
b
NB JN5 AU5
June 1986 Tillers
NB JN5 AU5
Au/Sp 1986 Tillers
Number of Tillers
210
180
150
120
90
60
30
0
a
a
a
a
a
b
b
b
a
NB JN5 AU5
Sp 1985 Tillers
NB NV5 MY6 JL6 AU6
Au/Sp 1986 Tillers

in shoot density in depressions. My trend in dry/wet yearly production of tillers seems to contradict this study. In addition, block differences, which would connote soil moisture influences, were not significant.

Tillering summary Overall, tiller production seems to track the phenology of the grasses. Burns are most detrimental during high growth periods: e.g., May for *P. pratensis* and August for *A. gerardii*. Some species are more sensitive to burning than others. No long terms effect was noted for *A. gerardii* or *S. nutans*, but *P. pratensis* seemed to show at least a two-year effect. *P. pratensis* also shows interactions between burning and both yearly rainfall pattern and site moisture.

Flowering

Warm season grasses *A. gerardii* flowered in response to weather conditions and fire. In 1985, the dry year, *A. gerardii* flowered only sparsely in unburned plots, but flowered much more in plots burned in May (Fig. 12). After a fire in June, *A. gerardii* flowered much later but produced almost as many flowering culms as those burned in May. In 1986, a wet year, the number of flowering culms/m^2 of *A. gerardii* was similar in Nov. 1985 and May 1986 burn plots and unburned plots. Flowering of *A. gerardii* after a July fire was delayed, and few flowering culms were produced. No flowering occurred after August burns in either year. During the second growing season after the burns, *A. gerardii* produced fewer flowering culms in the May 1985 burn plots than those burned in August 1985 and those left unburned (Fig. 13).

S. nutans had similar numbers of flowering culms in unburned plots and plots burned in May or November in either year (Fig. 14). Flowering of

Figure 12. Flowering of *Andropogon gerardii* in first growing season after burns (FBA=Flowering culms per basal area (m^{-2}), NB=No burn, MY5=May 1985 burn, JN5=June 1985 burn, AU5=August 1985 burn, NV5=November 1985 burn, MY6=May 1986 burn, JL6=July 1986 burn, AU6=August 1986 burn, error bars on columns indicate one standard error from mean, different letters above columns within a set indicate statistically different means)

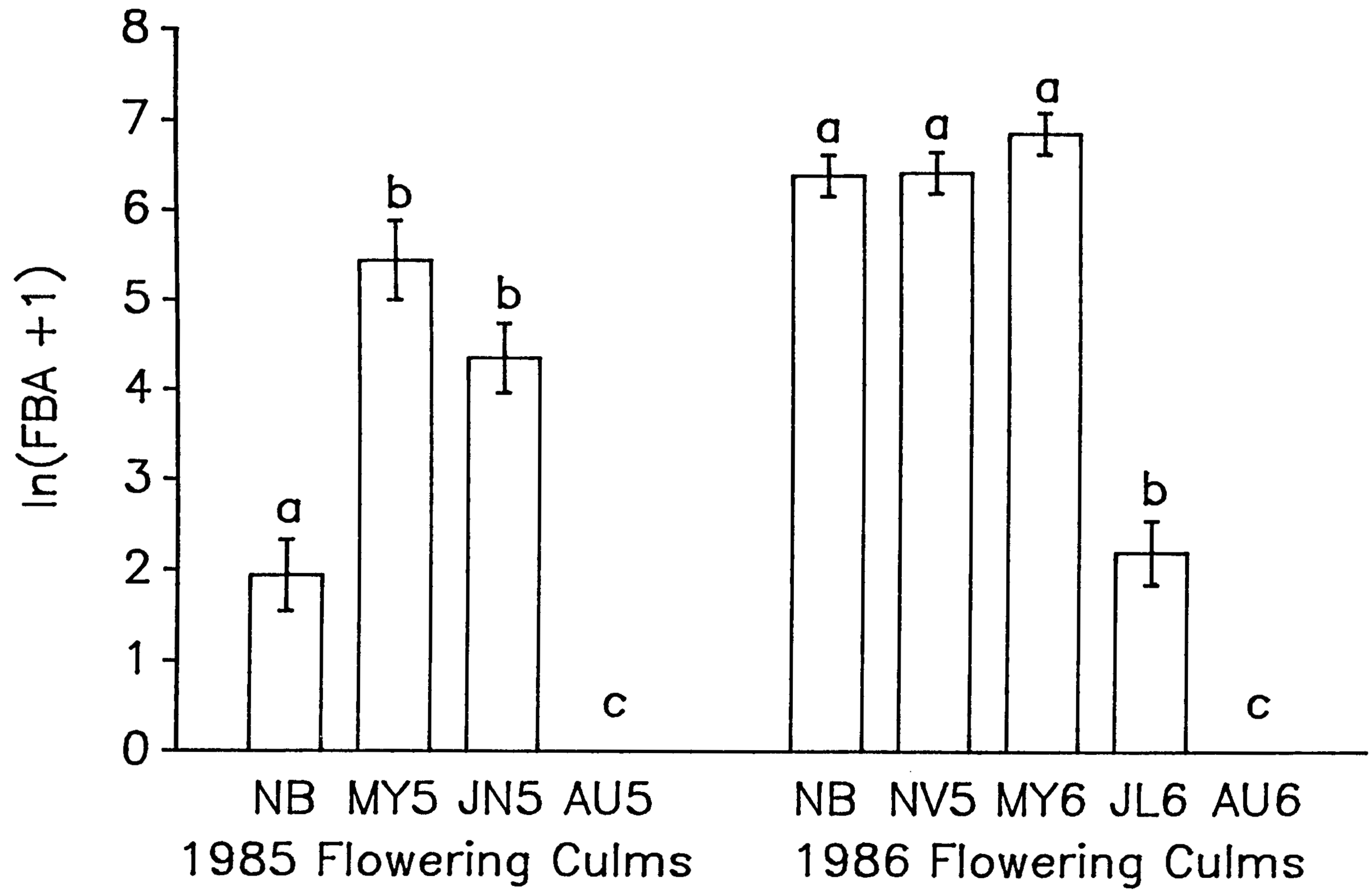

ln(FBA +1)
8
7
6
5
4
3
2
1
0
a
b
b
c
a
a
a
b
c
NB MY5 JN5 AU5
1985 Flowering Culms
NB NV5 MY6 JL6 AU6
1986 Flowering Culms

Figure 13. Flowering of <u>Andropogon gerardii</u> and <u>Sorghastrum nutans</u> in second growing season after burns (FBA=Flowering culms per basal area (m^{-2}), NB=No burn, MY5=May 1985 burn, JN5=June 1985 burn, AU5=August 1985 burn, error bars on columns indicate one standard error from means, different letters above columns within a set indicate statistically different means)

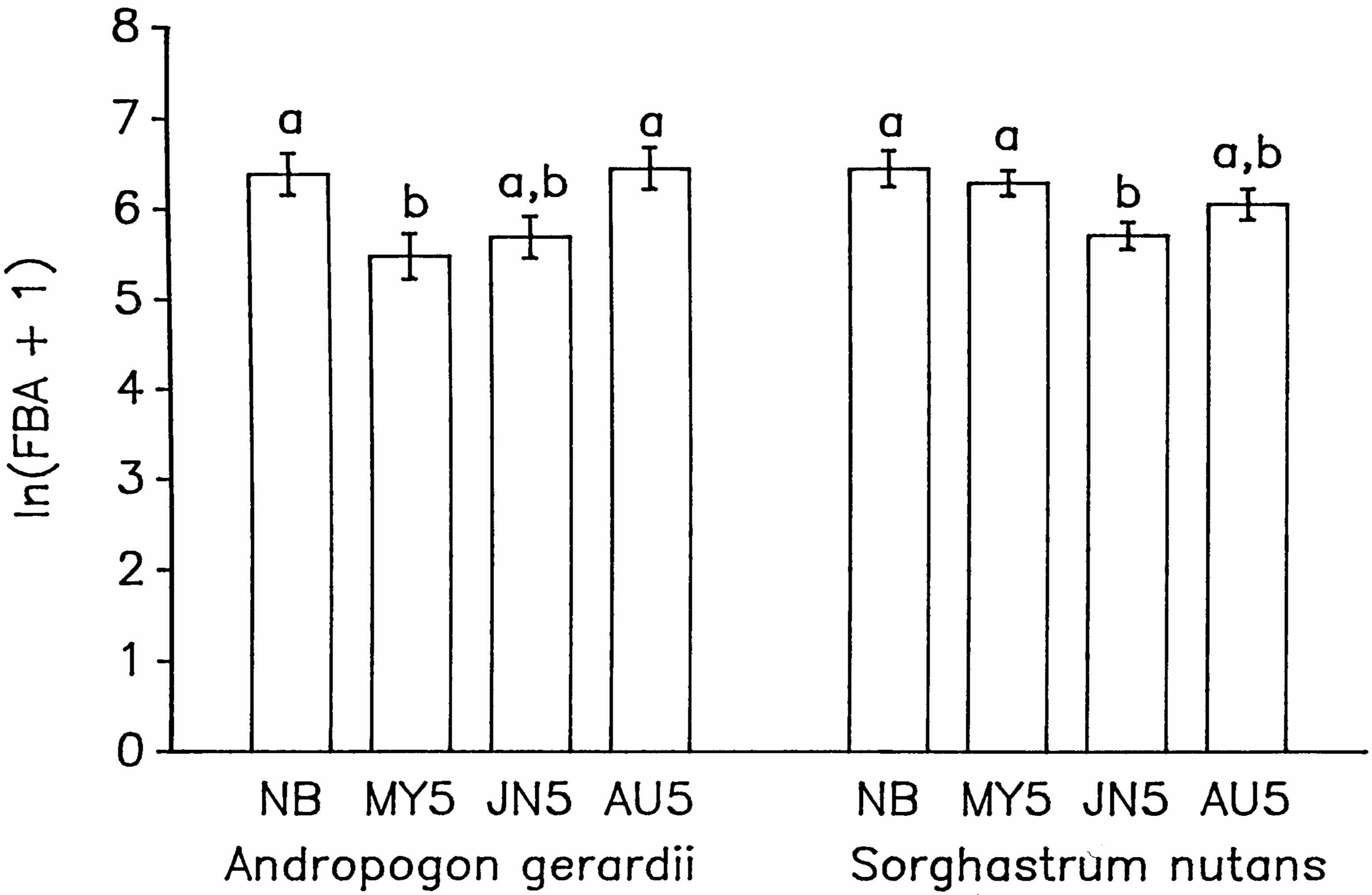
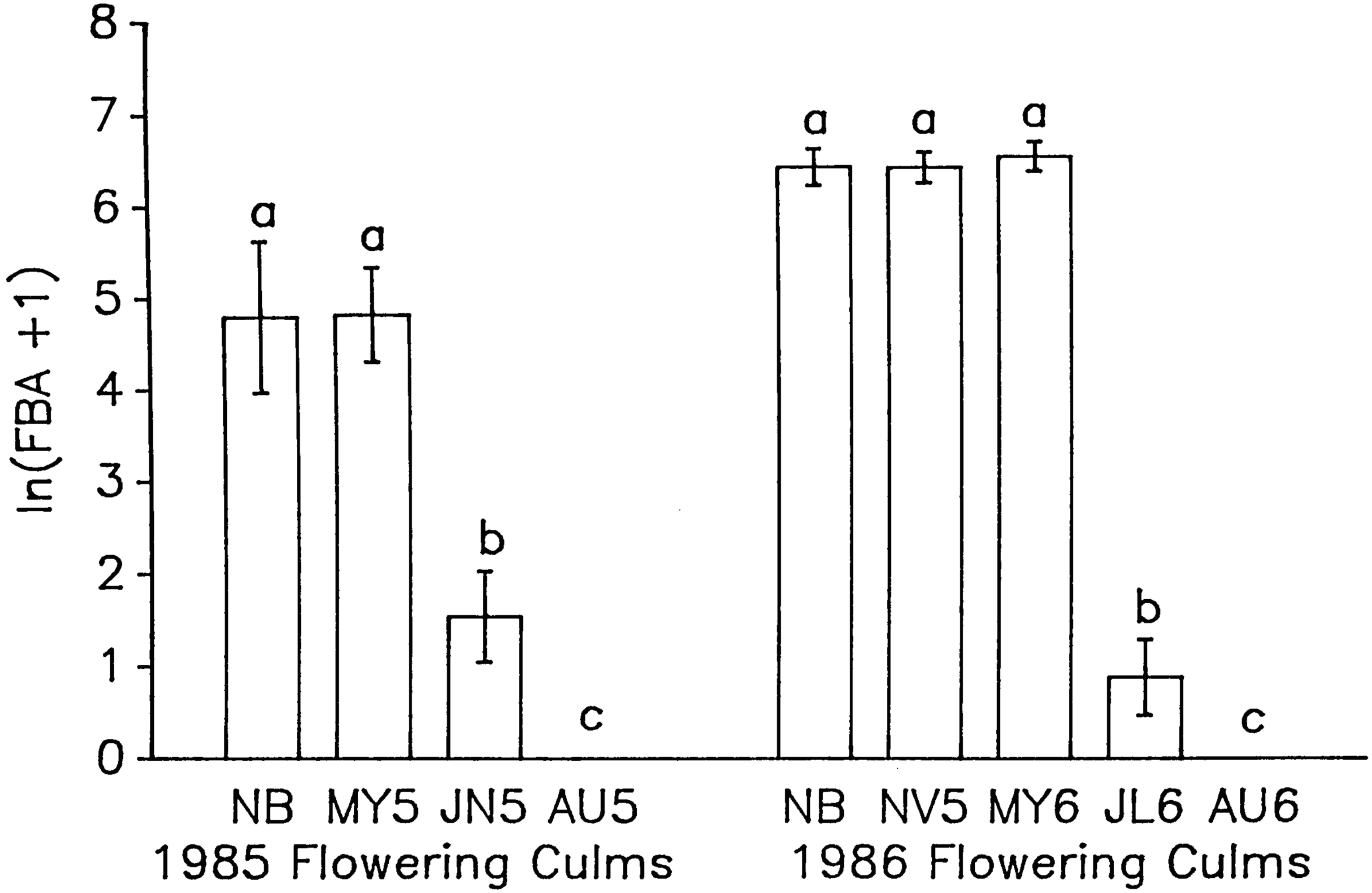

ln(FBA + 1)
8
7
6
5
4
3
2
1
0
a
b
a,b
a
a
a
b
a,b
NB MY5 JN5 AU5
Andropogon gerardii
NB MY5 JN5 AU5
Sorghastrum nutans

Figure 14. Flowering of *Sorghastrum nutans* in first growing season after burns (FBA=Flowering culms per basal area (m^{-2}), NB=No burn, MY5=May 1985 burn, JN5=June 1985 burn, AU5=August 1985 burn, NV5=November 1985 burn, MY6=May 1986 burn, JL6=July 1986 burn, AU6=August 1986 burn, error bars on columns indicate one standard error from mean, different letters above columns within a set indicate statistically different means)



ln(FBA +1)
0
1
2
3
4
5
6
7
8
a
a
b
c
a
a
a
b
c
NB MY5 JN5 AU5
1985 Flowering Culms
NB NV5 MY6 JL6 AU6
1986 Flowering Culms

S. nutans in plots burned in June 1985 and July 1986 was later, and few plants flowered. No flowering occurred after August burns. In the second growing season after the burns, S. nutans flowered significantly less in June 1985 burn plots than in May 1985 burn plots and unburned plots (Fig. 13). It is possible that the later exertion of growth and flowering during the first year may have detrimentally affected the clones of S. nutans in the June burn plots, so that flowering was reduced the following year.

In general, both A. gerardii and S. nutans delayed flowering after early or mid-summer burns and did not flower at all after August burns. S. nutans showed a reduction in flowering during the second growing season after the June 1985 burn, while A. gerardii had a reduction in plots burned in May 1985. A. gerardii showed a greater fire/weather pattern interaction than S. nutans to May burns. A. gerardii was stimulated to flower in the dry year with May burns. However, during the wet year, A. gerardii produced many flowering culms in unburned plots, as many as plots burned in November 1985 and May 1986.

Most studies have reported increased flower production of A. gerardii following spring burns (Aikman, 1955; Annala and Kapustka, 1982; Curtis and Partch, 1948, 1950; Dix and Butler, 1954; Ehrenreich and Aikman, 1957, 1963; Hadley and Kieckhefer, 1963; Hover and Bragg, 1981; Knapp and Hulbert, 1986; Kucera and Ehrenreich, 1962; Old, 1969; Peterson, 1983; Richards and Landers, 1973). Variation in this increase has been related to soil depth and weather patterns (Knapp and Hulbert, 1986) and soil moisture (Pemble et al. 1981). Only Rice and Parenti (1978), in Oklahoma, reported similar amounts of flowering culms of A. gerardii in unburned plots and following a spring (March) burn.

Reports of flowering of S. nutans following spring burns indicate variable responses. Some have reported greater flowering with burning (Annala and Kapustka, 1982; Ehrenreich and Aikman, 1957, 1963; Hadley and Kieckhefer, 1963; Knapp and Hulbert, 1986; Kucera and Ehrenreich, 1962, Old, 1969). Rice and Parenti (1978) reported no stimulation from burning, and Dix and Butler (1954) reported decreased flowering following burning. Density of flowering in a Kansas prairie has been greatest in wet years in clones growing in shallow soil, but amount of flowering did not correlate with depth of soil during dry years (Knapp and Hulbert, 1986). Flowering was greater than unburned plots only in wetter areas in northwestern Minnesota (Pemble et al. 1981).

A February burn in Iowa increased the number of flowering culms of A. gerardii in all plots and S. nutans in one plot, but in another plot, S. nutans had no more flowering culms than unburned plots (Aikman, 1955). In Illinois, both A. gerardii and S. nutans showed no difference in flowering between plots burned in December and unburned plots (Anderson and Van Valkenburg, 1977). My results from a November burn agrees with the results from the December burn in Illinois: i.e., A. gerardii and S. nutans flowered as much in unburned plots as in burned plots.

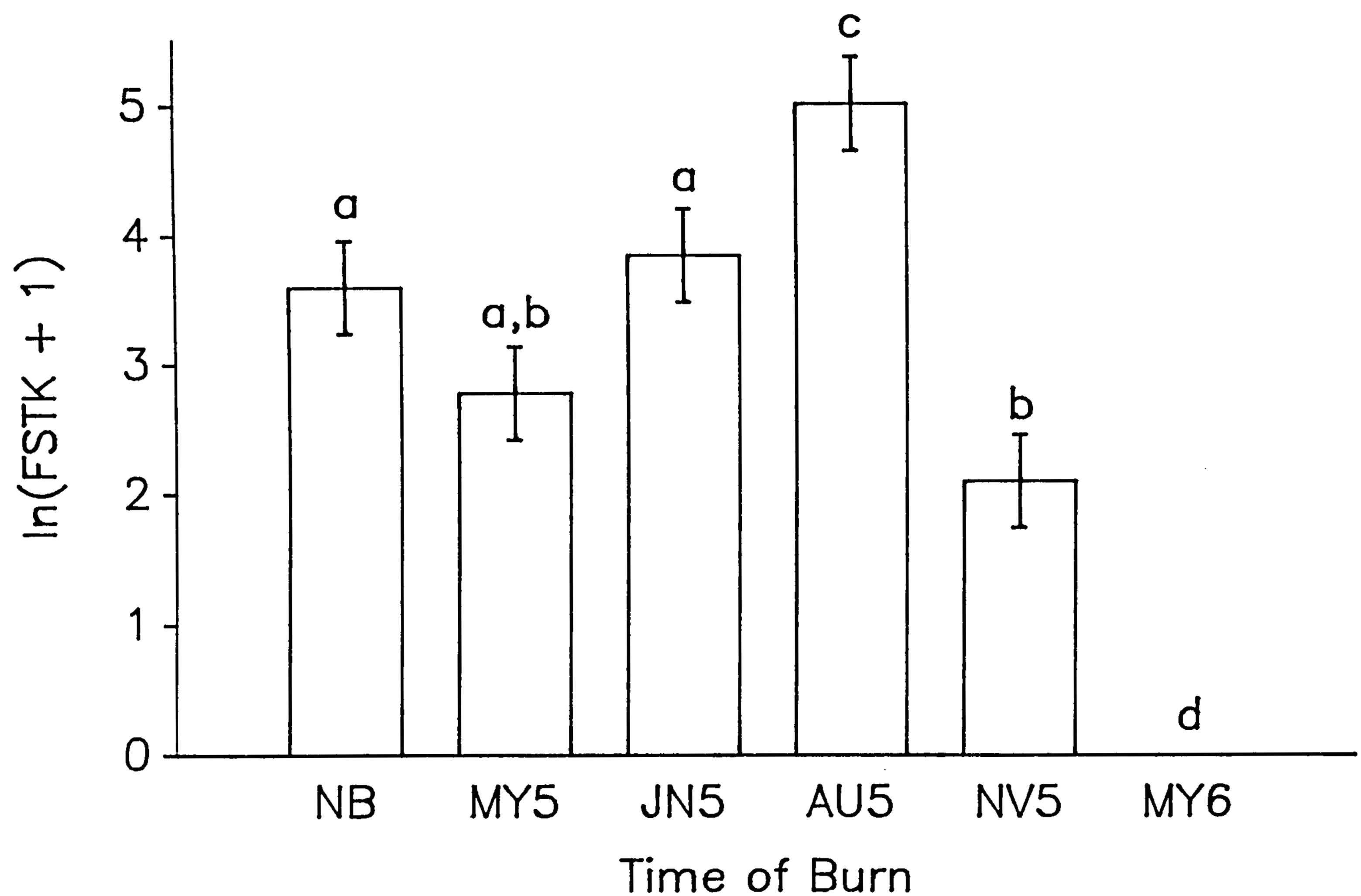
Flowering of some other warm season grasses, particularly Andropogon scoparius and Sporobolus heterolepis, is enhanced by spring or winter burning (Aikman, 1955; Dix and Butler, 1954; Ehrenreich and Aikman, 1957, 1963; Hover and Bragg, 1981; Knapp and Hulbert, 1986; Old, 1969; Richards and Landers, 1973). On the other hand, Dix and Butler (1954) reported that flowering of Bouteloua curtipendula was not enhanced by a spring burn.

In the second growing season after spring burns, both Dix and Butler (1954) and Hadley and Kieckhefer (1963) reported that A. gerardii still showed increased flowering over unburned plots. S. nutans either had a second year stimulation in flowering (Hadley and Kieckhefer, 1963) or no stimulation (Dix and Butler, 1954). My study showed a decrease in flowering of A. gerardii in the second year. This could have been due to the exertion of energy for flowering during a dry year, when unburned plots flowered little. Thus, the clones in each plot burned in May may have had lower energy reserves than those in unburned plots during the second growing season.

Poa pratensis Due to a dry spring, P. pratensis flowered little in 1985. In 1986, P. pratensis flowered profusely in August 1985 burn plots, significantly greater in number of flowering culms than all other treatments (Fig 15). June 1985 burn plots and unburned plots also had significantly more flowering culms than November burn plots. No flowering occurred in 1986 following the May 1986 burn.

Other studies have reported reduced flowering of P. pratensis following spring burns (Ehrenreich and Aikman, 1963; Richards and Landers, 1973). Curtis and Partch (1948) reported decreased flowering following a May burn, but no effect after October or March burns. Zedler and Loucks (1969) reported decreased flowering after spring burning on ridges, but increased flowering in depressions. Hover and Bragg (1981) reported that summer mowing increased flowering of Stipa spartea, another cool season grass.

Figure 15. Flowering in 1986 of Poa pratensis in response to burning (FSTK=Flowering culms per m^{-2}, NB=No burn, MY5=May 1985 burn, JN5=June 1985 burn, AU5=August 1985 burn, NV5=November 1985 burn, MY6=May 1986 burn, error bars on columns indicate one standard error from mean, different letters above columns indicate statistically different means)


ln(FSTK + 1)
5
4
3
2
1
0
a
a,b
a
c
b
d
NB
MY5
JN5
AU5
NV5
MY6
Time of Burn

Overall, flowering of _P. pratensis_ appears to be stimulated by late summer burns and harmed by fires occurring during spring and early summer high growth periods.

Flowering summary Flowering of _A. gerardii_ and _S. nutans_ was either delayed or did not occur at all after summer burns. Each species responded to spring fires in a unique manner. Flowering of _A. gerardii_ is usually enhanced by spring burning in a dry year, while _S. nutans_ blooms the same as unburned plots, despite the weather pattern. _S. nutans_, in general, has shown mixed results in response to being burned in the spring. Both species showed second year responses to timing of burning in the previous year. The reponse of flowering of _P. pratensis_ was also greatest after burning during a dormant growth period, although, for a cool season grass, this period was August. The previous year's burns had an effect on flowering production, with August burns having the greatest density of flowering culms, and reduced flowering following spring burns.

Seed production

In 1985, inflorescences of _A. gerardii_ contained a significantly higher number of caryopses in unburned plots than burn plots (Table 1). Since few flowering culms were present in unburned plots, each clone of _A. gerardii_ that did flower may have been able to support development of more fertilized embryos. On the other hand, _A. gerardii_, in plots burned in May, produced many more flowering culms and, as a result of the dry weather, may have aborted some fertilized embryos. In 1986, however, no difference in number of caryopses per inflorescence was found between treatments, although the number of seeds was much greater in this wet year than in

Table 1. Least-square means and standard errors of seeds per inflorescence of *Andropogon gerardii* in 1985

	Burn Date					
	No Burn		May 1985		June 1985	
	LS $\bar{X}$	s.e.	LS $\bar{X}$	s.e.	LS $\bar{X}$	s.e.
Plot Means	22.7	3.2	5.6	2.5	0.0	5.6
	1.5	3.9	2.6	2.5	6.0	5.6
	14.5	3.9	2.0	2.5	3.8	2.5
	12.0	3.9	6.0	2.5	0.0	2.5
			2.0	3.9	0.6	2.5
			7.6	2.5	0.0	2.5
					0.0	2.5
Treatment Mean	13.1	2.6	4.1	2.0	1.5	1.8

1985, a dry year (Table 2). No differences in number of caryopses per inflorescence were noted for S. nutans in either year, although, again, more seeds were produced per inflorescence in 1986 than 1985 (Tables 3, 4). P. pratensis also had no differences in number of caryopses per inflorescence between treatments in 1986 (Table 5). The number of caryopses per inflorescence was more variable between inflorescences than the mean caryopsis number between treatments.

Burton (1944) found that March and April burns stimulated seed production of Paspalum notatum and Cynodon dactylon in the southern U.S., but also found no treatment effect on the per cent of florets producing seeds. Thus, as in my study, seed production was based mainly on the number of flowering culms rather than on changes in caryopses per inflorescence. The number of caryopses per inflorescence in my study was related to weather conditions. Brown (1943) and Cornelius (1950) also reported that seed production of A. gerardii and other warm season grasses was related to weather conditions. Therefore, seed production is a function of the number of flowering culms and weather conditions.

Seedlings

Fewer seedlings grew in 1985, the dry year, than in 1986 (Tables 6, 7).

Monocots/dicots During both years, dicot seedlings outnumbered monocots, for all treatments. In 1985, only 34 monocot seedlings were found in the entire 6 block area (24 m^2), the equivalent of 1.4 seedlings m^{-2} (Table 6). These seedlings were scattered among all treatments and evenly

Table 2. Least-square means and standard errors of seeds per inflorescence of *Andropogon gerardii* in 1986

	Burn Date					
	No Burn		May 1985		June 1985	
	LS $\bar{X}$	s.e.	LS $\bar{X}$	s.e.	LS $\bar{X}$	s.e.
Plot Means	87.0	20.6	25.6	20.6	35.0	20.6
	15.0	26.6	38.0	26.6	17.0	20.6
	29.2	20.6	33.6	20.6	47.8	20.6
	82.8	20.6	66.4	20.6	123.4	20.6
	77.0	20.6	4.5	32.6	16.4	20.6
	66.8	20.6	79.4	20.6	34.4	20.6
	60.0	20.6	76.0	26.6	50.6	20.6
Treatment Mean	59.7	12.4	46.2	12.4	46.4	12.4
	Aug. 1985		Nov. 1985		May 1986	
	LS $\bar{X}$	s.e.	LS $\bar{X}$	s.e.	LS $\bar{X}$	s.e.
Plot Means	25.0	20.6	67.4	20.6	40.2	20.6
	57.7	26.6	13.2	20.6	0.0	46.2
	24.0	20.6	36.4	20.6	31.0	20.6
	60.2	20.6	56.4	20.6	125.8	20.6
	101.8	20.6	121.2	20.6	82.2	20.6
	92.8	20.6	38.6	20.6	68.8	20.6
	191.6	20.6	55.6	20.6	44.4	20.6
Treatment Mean	79.0	12.4	55.5	12.4	56.0	12.4

	July 1986	
	LS $\bar{X}$	s.e.
Plot Means	0.0	46.2
	7.4	20.6
	5.5	32.6
	5.5	23.1
	0.2	20.6
Treatment Mean	10.2	15.1

Table 3. Least-square means and standard errors of seeds per inflorescence of *Sorghastrum nutans* in 1985

	Burn Date					
	No Burn		May 1985		June 1985	
	LS $\bar{X}$	s.e.	LS $\bar{X}$	s.e.	LS $\bar{X}$	s.e.
Plot Means	37.4	13.3	13.0	13.3	0.0	29.7
	4.2	13.3	19.2	13.3	2.3	17.2
	66.5	14.9	13.6	13.3		
	31.8	14.9	1.2	13.3		
			21.4	13.3		
			97.4	13.3		
Treatment Mean	50.5	9.8	27.3	7.1	11.6	14.8

Table 4. Least-square means and standard errors of seeds per inflorescence of Sorghastrum nutans in 1986

	Burn Date					
	No Burn		May 1985		June 1985	
	LS $\bar{X}$	s.e.	LS $\bar{X}$	s.e.	LS $\bar{X}$	s.e.
Plot Means	87.4	28.1	65.6	28.1	58.4	28.1
	33.6	28.1	47.6	28.1	67.8	28.1
	170.2	28.1	96.0	28.1	93.2	28.1
	81.4	28.1	115.0	28.1	51.2	28.1
			88.2	28.1	193.6	28.1
			119.2	28.1	89.0	28.1
			241.8	28.1	45.6	28.1
Treatment Mean	105.6	23.2	110.5	16.7	85.5	16.7
	Aug. 1985		Nov. 1985		May 1986	
	LS $\bar{X}$	s.e.	LS $\bar{X}$	s.e.	LS $\bar{X}$	s.e.
Plot Means	104.0	28.1	59.0	28.1	47.6	28.1
	22.0	28.1	45.4	28.1	57.2	28.1
	63.4	28.1	94.6	28.1	92.0	28.1
	57.2	28.1	71.6	28.1	161.8	28.1
	105.2	31.4	144.2	28.1	62.8	28.1
	120.8	28.1			129.6	28.1
Treatment Mean	78.6	18.5	86.3	20.4	91.7	18.5

	July 1986	
	LS $\bar{X}$	s.e.
Plot Means	0.0	28.1
Treatment Mean	-8.5	47.5

Table 5. Least-square means and standard errors of seeds per inflorescence of Poa pratensis in June 1986

	Burn Date					
	No Burn		May 1985		June 1985	
	LS $\bar{X}$	s.e.	LS $\bar{X}$	s.e.	LS $\bar{X}$	s.e.
Plot Means	150.4	38.4	263.0	38.4	126.6	38.4
	129.2	38.4	243.5	43.0	147.0	38.4
	141.4	38.4	182.6	38.4	182.8	38.4
	225.8	38.4	161.4	38.4	211.0	38.4
	129.0	38.4	124.0	60.8	162.2	38.4
	185.6	38.4	238.8	38.4	294.4	38.4
	322.6	38.4	174.8	38.4	119.6	38.4
Treatment Mean	183.4	20.6	198.3	20.6	177.6	20.6

	Aug. 1985		Nov. 1985	
	LS $\bar{X}$	s.e.	LS $\bar{X}$	s.e.
Plot Means	191.6	38.4	292.2	38.4
	198.4	38.4	205.7	49.6
	150.8	38.4	255.0	85.9
	179.2	38.4	295.2	38.4
	138.0	38.4	286.2	38.4
	265.6	38.4	221.0	85.9
	178.4	38.4	191.8	38.4
Treatment Mean	186.0	20.6	249.6	20.6

Table 6. Number of monocot (M) and dicot (D) seedlings per m^2 present in Fall 1985 in burned and unburned plots

	Date of Burn							
	No Burn		May 85		June 85		Aug. 85	
Block	M	D	M	D	M	D	M	D
A	7	20	2	6	1	16	0	0
B	0	74	2	9	0	1	0	1
C	0	109	1	4	0	1	0	4
D	0	2	0	1	2	2	5	2
E	0	19	4	11	7	0	0	0
F	0	13	0	8	2	7	1	3
G	0	3	X	X	0	6	8	2
Total[a]	7	237	9	39	12	27	6	10

[a]Total does not include block G because of missing data.

distributed between warm season grasses, Panicum scribnerianum, and P. pratensis.

During 1986, 275 monocot seedlings were found, or 5.7 seedlings m-2 (Table 7). The lowest number of monocots were found in unburned plots. The highest counts were in August 1985, November 1985, and May 1986 burn plots. Most of the monocot seedlings in 1986 were P. scribnerianum.

In 1985, unburned plots tended to have more dicots, but there was great variability in number between plots (Table 6), due to the structure and amount of thatch. June 1985 and August 1985 burn plots had fewest dicot seedlings; the reduction after fire was mainly due to a decrease in the biennials. In 1986, the highest counts of dicots were taken in May 1985, June 1985, and August 1985 burn plots (Table 7). In other words, burning in one year (1985) stimulated germination in the second. July 1986 burn plots had the least number of dicots in 1986.

Annual/biennial/perennial Few seedling of annuals were present in either year (Tables 8, 9). Numbers of biennial verses perennial seedlings showed no significant pattern in unburned plots in 1985 (Table 8). Fewer biennial than perennial seedlings occurred in the burned plots in 1985. In 1986, however, greater numbers of biennial seedlings than perennial seedlings grew in unburned plots (Table 9).

Comparing between treatments, the highest numbers of biennial seedlings in 1985 were in unburned plots (Table 8). In 1986, May 1985 and June 1985 burn plots had the most biennial seedlings, while July 1986 burn plots had the least (Table 9). Also in 1986, the greatest numbers of perennial seedlings occurred in May 1985 burn plots, and the least in July

Table 7. Number of monocot (M) and dicot (D) seedlings per m^2 present in Fall 1986 in burned and unburned plots

	Date of Burn							
	No Burn		May 85		June 85		Aug. 85	
Block	M	D	M	D	M	D	M	D
A	2	160	11	280	7	130	9	158
B	1	74	6	248	1	494	2	162
C	0	48	1	88	8	126	12	130
D	0	6	0	72	0	78	9	42
E	2	18	6	88	11	66	12	56
F	0	10	2	100	3	94	19	120
G	1	4	X	X	0	12	12	42
Total[a]	5	316	26	876	30	988	63	668
	Nov. 85		May 86		July 86		Aug. 86	
Block	M	D	M	D	M	D	M	D
A	3	58	7	76	3	20	5	4
B	16	84	12	84	4	18	2	2
C	2	36	10	90	4	14	1	4
D	3	100	6	30	8	2	0	152
E	32	60	10	34	3	12	9	108
F	4	180	4	80	1	28	2	12
G	0	26	14	24	2	158	X	X
Total[a]	60	518	49	394	23	94	19	282

[a]Total does not include block G because of missing data.

Table 8. Number of annual (A), biennial (B), and perennial (P) seedlings per m2 marked in 1985 and present in June 1986 in burned and nonburned plots (U=unknown seedlings, X=missing value)

	Date of Burn															
	No Burn				May 85				June 85				Aug 85			
BLK	A	B	P	U	A	B	P	U	A	B	P	U	A	B	P	U
A	0	6	7	1	1	3	1	0	0	0	11	0	0	0	0	0
B	0	15	10	0	0	0	6	0	0	1	0	0	0	1	0	0
C	0	5	59	0	0	0	5	0	0	0	1	0	0	0	3	0
D	0	1	0	0	0	0	1	0	0	0	1	0	0	0	2	0
E	0	2	5	1	0	1	13	0	0	0	6	0	0	0	0	0
F	0	7	2	0	0	0	4	0	0	2	3	0	0	1	2	0
G	0	2	0	0	X	X	X	X	0	0	1	0	0	0	6	0
Ta	0	36	83	2	1	4	30	0	0	3	22	0	0	2	7	0

aTotal does not include block G because of missing data.

Table 9. Number of annual (A), biennial (B), and perennial (P) seedlings per m^2 present in Fall 1986 in burned and nonburned plots (U=unknown seedlings, x=missing values)

	Date of Burn															
	No Burn				May 85				June 85				Aug. 85			
BLK	A	B	P	U	A	B	P	U	A	B	P	U	A	B	P	U
A	0	154	8	0	10	188	87	6	8	54	69	6	2	140	17	8
B	0	58	13	4	10	216	22	6	2	478	15	0	8	140	8	8
C	10	24	14	0	0	40	49	0	4	94	24	12	38	40	58	6
D	0	6	0	0	0	18	52	2	0	66	4	8	0	10	33	8
E	0	14	6	0	6	22	64	2	2	34	39	2	0	16	52	0
F	0	10	0	0	0	52	48	2	2	72	21	2	6	86	43	4
G	0	4	1	0	X	X	X	X	0	6	6	0	2	24	26	2
Ta	10	266	41	4	26	536	322	18	18	733	172	30	54	432	211	34
	Nov. 85				May 86				July 86				Aug. 86			
	A	B	P	U	A	B	P	U	A	B	P	U	A	B	P	U
A	0	42	11	8	2	62	19	0	0	12	7	4	0	2	5	2
B	4	46	42	8	6	16	72	2	0	2	10	10	0	0	2	2
C	6	6	24	2	12	14	66	8	0	4	10	4	0	2	1	2
D	12	42	41	8	0	6	28	2	0	2	8	0	0	114	2	36
E	0	38	52	2	6	20	18	0	0	0	5	10	0	102	15	0
F	8	148	22	6	38	14	16	16	5	10	0	14	0	4	4	6
G	0	2	24	0	2	6	30	0	131	20	5	4	X	X	X	X
Ta	30	322	192	34	64	132	219	28	5	30	40	42	0	224	29	48

[a]Total does not include block G because of missing data.

1986 and August 1986 burn plots, and unburned plots. Therefore, many biennial and perennial seedlings grew during the second growing season.

Native/nonnative Comparing within treatments, in 1985, May burn plots had more seedlings of native species than nonnative (Table 10). June 1985 burn plots and unburned plots had fewer native than nonnative seedlings in 1986 (Table 11).

No difference between treatment was noted in native seedlings counts in 1985 (Table 10). In 1986, however, May burn plots of both 1985 and 1986 had higher counts of seedlings of native species than August 1986 burn plots and unburned plots (Table 11). Seedlings of nonnative species were greatest in unburned plots and least in August 1985 burn plots in 1985. In 1986, June 1985 burn plots had the greatest number of nonnative seedlings, and July 1986 burn plots had the least. Therefore, burning, particularly in spring, increases the native species component of seedlings, but nonnative species are encouraged in the burned plots the following year.

Individual species Three patterns of species' responses to fires were evident from the 1986 seedlings. First, a number of species germinated (in 1986) mostly in plots burned in 1985, and also in unburned plots. Aster azureus, Daucus carota, Lactuca serriola, Medicago lupulina, Melilotus alba, Pastinaca sativa, Trifolium repens, Viola pedatifida, and Poa pratensis are examples of this group (Table 12a-h, Table 13a). Second, some species germinated primarily in bothe 1985 and 1986 burned plots. Examples of these species are Oxalis stricta, Verbena stricta, Panicum scribnerianum, and warm season grasses (Table 12i-j, Table13b-c). (Note: A few warm season grass seedlings were found in an unburned plot in 1985, but this was in an area of little thatch and low phytomass.) Third, one genus,

Table 10. Number of 1985 native (NAT) and nonnative (NON) seedlings per m^2 marked in 1985 and present in June 1986 in burned and nonburned plots (U=unknown seedlings)

	Date of Burn											
	No Burn			May 85			June 85			Aug. 85		
BLK	NAT	NON	U	NAT	NON	U	NAT	NON	U	NAT	NON	U
A	7	6	1	4	1	0	11	0	0	0	0	0
B	9	16	0	6	1	0	0	1	0	0	1	0
C	59	5	0	3	2	0	1	0	0	3	0	0
D	0	1	0	1	0	0	0	1	0	2	0	0
E	5	2	1	11	3	0	4	2	0	0	0	0
F	4	5	0	4	0	0	3	2	0	2	1	0
G	0	2	0	X	X	X	1	0	0	6	0	0
T[a]	84	35	2	29	7	0	19	6	0	7	2	0

[a]Total does not include block G because of missing data.

Table 11. Number of native (NAT) and nonnative (NON) seedlings per m^2 marked in 1986 and present in Fall 1986 in burned and nonburned plots (U=unknown seedlings)

	Date of Burn											
	No Burn			May 85			June 85			Aug. 85		
BLK	NAT	NON	U	NAT	NON	U	NAT	NON	U	NAT	NON	U
A	7	155	0	79	208	4	54	77	6	14	145	8
B	13	58	4	12	238	4	4	491	0	8	150	6
C	12	36	0	42	47	0	13	109	12	47	103	2
D	0	6	0	52	18	2	4	72	2	29	22	0
E	2	18	0	50	42	2	23	52	2	24	44	0
F	0	10	0	40	60	2	20	75	2	34	101	4
G	0	5	0	X	X	X	4	8	0	24	28	2
Ta	34	283	4	275	613	14	118	876	24	156	565	20

	Nov. 85			May 86			July 86			Aug. 86		
	NAT	NON	U	NAT	NON	U	NAT	NON	U	NAT	NON	U
A	12	43	6	25	58	0	12	7	4	4	3	2
B	44	54	2	65	29	2	15	3	4	2	0	2
C	12	26	0	70	26	4	12	4	2	3	0	2
D	7	90	6	32	2	2	7	3	0	2	114	36
E	47	45	0	23	21	0	9	2	4	11	106	0
F	24	156	4	45	25	14	4	13	12	4	4	6
G	26	0	0	26	12	0	7	149	4	X	X	X
Ta	146	414	18	260	161	22	59	32	26	26	227	48

[a]Total does not include block G because of missing data.

Table 12. Number of seedlings per 0.5 m^2 marked in 1986 and present in Fall 1986 in burned and nonburned plots (x=missing value; all blanks are zeros)

a. Aster azureus

	Date of Burn							
Block	NB	My85	Jn85	Au85	Nv85	My86	Jl86	Au86
A	1	36	18	2				
B	5	4	1	1	2	4		
C	3	14	2	5	1	19		
D		26	2			2		
E		10			1	1		3
F		16	4		2			1
G		x		3	11			x

b. Daucus carota

	Date of Burn							
Block	NB	My85	Jn85	Au85	Nv85	My86	Jl86	Au86
A	68	70	23	62	15	24		
B	21	93	230	53	17	5		
C	8	5	35	14	2	5		
D	3		22	1	17	1	1	34
E	4	2	3	3	11	1		2
F	1			5	4	5	1	
G	1	x		4				x

c. Lactuca serriola

	Date of Burn							
Block	NB	My85	Jn85	Au85	Nv85	My86	Jl86	Au86
A	8	5	3	4	2	2		1
B	7	15	9	16	2	1	1	
C	2	10	10	4	1	1	2	
D		9	9	4	4			23
E		5	14	5	6	2		49
F		5	3	6	2	1	4	1
G		x	2	8		2	8	x

Table 12. (continued)

d. *Medicago lupulina*

Block	Date of Burn							
	NB	My85	Jn85	Au85	Nv85	My86	Jl86	Au86
A		5	4	1		1		
B		5	1	4	2	3		
C	5		2	19	3	6		
D					6			
E		3	1			3		
F			1	3	4	3	1	
G		x						x

e. *Melilotus alba*

Block	Date of Burn							
	NB	My85	Jn85	Au85	Nv85	My86	Jl86	Au86
A		17	1	4				
B					1			
C	2	2		1				
D								
E	2	3				3		
F		20	28	30	64			1
G		x						x

f. *Pastinaca sativa*

Block	Date of Burn							
	NB	My85	Jn85	Au85	Nv85	My86	Jl86	Au86
A	1	2				1	3	
B	1					1		
C		3		2				
D			2					
E	1	1			1			
F	4	1	5	2	1			
G	1	x	1		1	1		x

Table 12. (continued)

g. Trifolium repens

Block	NB	My85	Jn85	Au85	Nv85	My86	Jl86	Au86
				Date of Burn				
A			5	3		1		
B		3	6	1	2	2		
C	1	3	4	11	7			
D				2	17			
E	1	6	8	14	3			
F		3		3	1	2		
G		x	1	2		2		x

h. Viola pedatifida

Block	NB	My85	Jn85	Au85	Nv85	My86	Jl86	Au86
				Date of Burn				
A	2	2		1	1			
B	1							
C	1	3	2	2				
D				8				
E	1	7	3	2		2		
F		1	2	2	3	1		
G		x		2				x

i. Oxalis stricta

Block	NB	My85	Jn85	Au85	Nv85	My86	Jl86	Au86
				Date of Burn				
A						5	2	2
B					6	18		
C				2	2	6		
D					2	7		1
E		1	1	1		1	5	
F			2	6	3		2	
G		x	1		1	4		x

Table 12. (continued)

j. *Verbena stricta*

				Date of Burn				
Block	NB	My85	Jn85	Au85	Nv85	My86	Jl86	Au86
A								
B				1		1		
C		1						
D		1						
E					1			
F				1	1			
G		x						x

k. *Cirsium* sp.

				Date of Burn				
Block	NB	My85	Jn85	Au85	Nv85	My86	Jl86	Au86
A					4	4	3	
B				1	3	1		
C					1	1		1
D						2		
E					1	4		
F					3	1		
G		x			1		1	x

Table 13. Number of seedlings per m^2 marked in 1986 and present in Fall 1986 in burned and nonburned plots (x=missing value; all blanks are zeros)

a. Poa pratensis

	Date of Burn							
Block	NB	My85	Jn85	Au85	Nv85	My86	Jl86	Au86
A	1	8	5	3	1			1
B		4	1		4	1	1	
C		1	3	1				
D								
E	2	2			1	3		3
F		2	1	3	2	2		
G	1	x						x

b. Panicum scribnerianum

	Date of Burn							
Block	NB	My85	Jn85	Au85	Nv85	My86	Jl86	Au86
A		1	1	3	1	2	1	4
B	1	2			6	1		2
C			2	8		8	2	1
D				9	3	2	4	
E		4	11	12	31	1	1	2
F			2	15	1			
G		x		12		5		x

c. Warm Season Grasses

	Date of Burn							
Block	NB	My85	Jn85	Au85	Nv85	My86	Jl86	Au86
A	1	2	1	3	1	2		
B				2	6	8		
C				3		2		
D						3		
E						5		
F				1	1	1		
G		x						x

Cirsium, germinated only in plots burned in November 1985 or in 1986 (Table 12m).

Aster azureus, Daucus carota, and Lactuca serriola (Table 12a-c) contributed greatly to the overall second year effect. These species were found in high numbers during 1986 in 1985 burn plots.

Individual species also showed great variability in number of seedlings within each plot. This was likely due to specific plot conditions within a block and to patchy distribution of seeds from local seed sources. All species showed this phenomena, but Daucus carota, Lactuca serriola, and Melilotus alba (Table 12b, c, e) are striking examples.

Survivorship Thirty-four monocot seedlings (mostly grasses) were found in 1985. In June 1986, 30 were relocated, of which 23 were still living, the equivalent of 77% survival. By September 1986, 29 were relocated, but only 17 seedlings still lived. Thus, the maximum minimal survival was 59%; in September 1986, 0.8 monocot seedlings per m^2 from 1985 remained. Dicot survivorship varied from 0 to 100%, and no treatment enhanced survivorship better than another (Table 14). Overall, dicot survivorship was 49%. If this is an accurate estimate, then 49% of the 324 original Fall 1985 seedlings is 158.8 seedlings left in Fall 1986, or 5.9 seedlings per m^2.

Seedling discussion In general, few monocots germinated, but burning enhanced the number of monocot seedlings. Burning reduced the number of biennials during the first year, but stimulated germination the following fall and spring. More perennial seedlings were found in burned plots, and they showed a second year stimulation. Burning, particularly in May, enhanced growth of native seedlings, but nonnative seedlings were

Table 14. Per cent survival of dicot seedlings marked in 1985

			Time of Observation					
			June 1986			Sept. 1986		
Burn Date	Block	# Fall 1985	# tees found	# living plants	% surv.	# tees found	# living plants	% surv.
No Burn	A	20	21	12	57	20	7	35
	B	74	49	25	51	49	14	28
	C	109	96	64	67	80	40	50
	D	2	2	1	50	1	1	50
	E	19	14	8	57	9	4	44
	F	13	9	8	89	6	3	50
	G	3	2	2	100	1	0	0
May 1985	A	6	6	4	67	6	5	67
	B	9	7	6	86	6	6	86
	C	4	4	4	100	4	3	75
	D	1	1	1	100	1	1	100
	E	11	11	11	100	9	9	100
	F	8	8	4	50	8	1	12
	G	x	x	x	x	x	x	x
June 1985	A	16	11	10	91	8	8	73
	B	1	1	1	100	1	1	100
	C	1	2	1	50	2	1	50
	D	2	2	1	50	2	1	50
	E	0						
	F	7	6	4	67	3	1	33
	G	6	2	1	50	1	1	50
Aug. 1985	A	0						
	B	1	1	1	100	1	0	0
	C	4	4	3	75	3	2	67
	D	2	0	0	0	0	0	0
	E	0						
	F	3	3	2	67	2	1	50
	G	2	1	0	0	1	0	0

abundant in the second year. Species had unique responses to the time of fire. The spatial heterogeneity of seed distribution and uniqueness (i.e., the height of phytomass which would influence seed deposition, the amount of light at ground surface, and soil moisture) of each burn treatment to seedling development created variation in seedling establishment, which was unresolved by blocking techniques.

Blake (1935) reported that germination in a tallgrass prairie occurs mainly in fall and spring. Monocots in the seed bank of an Illinois prairie were only 20% of the total number of seeds (Johnson and Anderson, 1986). Rabinowitz (1981) reported that 70% of the seedlings in her seed bank study of a prairie in Missouri were monocots, but 83% of those were _Juncus tenuis_. So, low numbers of monocot seedlings in my study may be due to low numbers of monocot seeds. (_Juncus_ spp. were very low components of my prairie and relatively distant from my experimental area.) In addition, because of the dryness in 1985, few grass seeds were added that year to the seed bank.

Other studies of seedling development after fire have reported various results according to the species investigated. In Iowa, higher numbers of small juveniles of _Dodecatheon meadia_ were found in burned areas than unburned areas (Leoschke, 1986). Timing and frequency of burning has shown trends of affecting establishment of _Melilotus alba_ (Kline, 1986). Curtis and Partch (1948), in Wisconsin, reported that _A. gerardii_ seedlings increased after spring burns. Lippert and Hopkins (1950) found that the number of _Sporobolus cryptandrus_ seedlings in burned areas was six times that of unburned in a natural revegetated habitat near Hays, Kansas, but that no seedlings of _Bromus tectorum_ occurred on burned sites. Owensby and

Launchbaugh (1977) also reported that the weedy species Aristida oligantha and Bromus japonicus produced fewer seedlings in areas burned in fall, than in unburned areas. Scanlan and O'Rourke (1982) and Shaw (1957) have also reported that grass seedlings increased following spring burns in Australia.

Bakker et al. (1980) found that the time of haymaking in a Netherlands grassland had an impact on the survivorship of seedlings. More monocots survived to juvenile stage with July mowing, but more dicots survived to juvenile stage with September mowing.

In summary, burning enhances the introduction of new plants. The time of burn can also be important to seedling establishment. Since species are unique in their responses to fires, potential changes in the prairie composition could result from burning.

CONCLUSIONS

The effect of fire at different times of the year is related to the phenology of the plants involved. The effect of fires on tillering, flowering, and seed production tracked the growth phase of the grasses. Tillering and flowering of _A. gerardii_ and _S. nutans_ (warm season grasses) were enhanced by fall or spring burns and were reduced as the season continued. _P. pratensis_, on the other hand, was detrimentally affected by spring or early summer burns. Flowering of _P. pratensis_ was enhanced by an August burn.

Responses of the grasses to fire are species specific. For instance, _A. gerardii_ and _S. nutans_ flowered in different patterns in relation to spring burns. Flowering of _A. gerardii_ was stimulated by a May burn in a dry year, but during a wet year flowering production was equivalent in May burn plots and unburned plots. On the other hand, _S. nutans_ was not stimulated by spring burning in either year. Thus, _A. gerardii_ appeared to be more sensitive to both weather conditions and fire, while flowering of _S. nutans_ was not affected by May burning. _P. pratensis_ has shown its sensitivity to spring fires in many situations. However, because it is not native to this region, it may be more sensitive than other cool season grasses which native to this prairie region. Therefore, study on other cool season grasses would be insightful.

The effects of timing of fire on tillering disappeared at the end of the second growing season. This means that the time of fire will not have long-term effects for _A. gerardii_ and _S. nutans_. However, the effects of repeated yearly burning at various time of year may need to be investigated.

Seed production was a function of weather pattern (particularly rainfall) and the number of flowering culms produced. In turn, the number of flowering culms was influenced by fire and the timing of that fire. The number of seeds produced would influence the availability of seedling recruits.

Seedling establishment was enhanced by burning. Species responded individually to the burns, but some general effects were noted. Fewer biennial seedlings and nonnative seedlings were present in burned plots the first growing season, but greater numbers were found in the second growing season. Burning enhanced the establishment of perennials and native seedlings. Therefore, burning enhanced the establishment of new plants which, in turn, could change the composition of the prairie community.

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APPENDIX A: LIST OF SPECIES PRESENT IN PRAIRIE OF EXPERIMENTAL SITE

Asclepiadaceae
- Asclepias incarnata
- Asclepias syriaca
- Asclepias verticillata
- Asclepias viridiflora

Boraginaceae
- Lithospermum canescens

Caprifoliaceae
- Sambucus canadensis

Chenopodiaceae
- Chenopodium hybridum

Commelinaceae
- Tradescantia bracteata

Compositae
- Ambrosia artemisiifolia
- Ambrosia trifida
- Artemisia ludoviciana
- Aster azureus
- Aster ericoides
- Aster pilosus
- Circium altissimum
- Circium discolor
- Echinacea pallida
- Erigeron annuus
- Erigeron strigosus
- Lactuca serriola
- Rudbeckia hirta
- Senecio congestus
- Solidago canadensis
- Solidago missouriensis

Cruciferae
- Thlaspi arvense

Cyperaceae
- Carex amphibola var. turgida
- Carex brevior
- Carex lasiocarpa var. latifolia
- Carex meadii
- Carex aff. molesta
- Scirpus atrovirens

Euphorbiaceae
- Euphorbia corollata
- Euphorbia maculata

Equisetaceae
- Equisetum laevigatum
- Equisetum arvense

Gentianaceae
- Gentiana puberula

Gramineae
- Agropyron repens
- Agrostis alba
- Andropogon gerardii
- Andropogon scoparius
- Bouteloua curtipendula
- Bromus inermis
- Elymus aff. riparius
- Elymus virginicus
- Muhlenbergia cuspidata
- Muhlenbergia frondosa
- Panicum scribnerianum
- Phalaris arundinacea
- Phleum pratense
- Poa pratensis
- Setaria lutescens
- Sorghastrum nutans
- Spartina pectinata
- Sporobolus heterolepis
- Stipa spartea

Iridaceae
- Sisyrinchium campestre

Juncaceae
- Juncus dudleyi
- Juncus tenuis

Labiatae
- Lycopus americanus
- Mentha arvensis
- Monarda fistulosa
- Scutellaria lateriflora
- Scutellaria leonardi
- Stachys palustris
- Teucrium canadense

Leguminosae
- Amorpha canescens
- Desmodium illinoense
- Lespedeza capatata
- Medicago lupulina
- Melilotus alba
- Petalostemum candidum
- Petalostemum purpureum
- Trifolium pratense
- Trifolium repens
- Vicia americana

Moraceae
- Cannabis sativa
- Morus sp.

Onagraceae
- Oenothera biennis

Oxalidaceae
- Oxalis stricta
- Oxalis violacea

Polygonaceae
- Polygonum convolvulus
- Polygonum pensylvanicum

Primulaceae
- Lysimachia ciliata

Portulacaceae
- Portulaca oleracea

Ranunculaceae
- Anemone canadensis
- Anemone cylindrica

Rosaceae
- Agromonia striata
- Fragaria virginiana
- Geum laciniatum
- Potentilla norvegica
- Potentilla simplex
- Prunus americana
- Rosa blanda
- Rosa carolina X suffulta

Scrophulariaceae
- Mimulus ringens
- Veronica catenata
- Veronicastrum virginicum

Solanaceae
- Physalis heterophylla
- Physalis longifolia
- Physalis virginiana
- Solanum nigrum

Umbelliferae
- Daucus carota
- Pastinaca sativa

Verbenaceae
- Verbena hastata
- Verbena stricta
- Verbena urticifolia

Violaceae
- Viola pedatifida

APPENDIX B:

TOPOGRAPHICAL AND SOIL CONDITIONS AT EXPERIMENTAL SITE

Table B1. Topographic and soil conditions at experimental site:
1. Slope and direction of blocks

Block	Slope Angle	Direction of Slope	Direction Block with Slope
A	9	70	78
B	10	70	77
C	11	65	67
D	10	55	44
E	8	47	40
F	7	38	38
G	13	66	47

Figure B1. Topographic and soil conditions at experimental site:
2. Depth (cm) of mollic colors in soil horizon (numbers in parantheses indicate depth of mollic colors in at least one half of matrix, letters represent block designations)

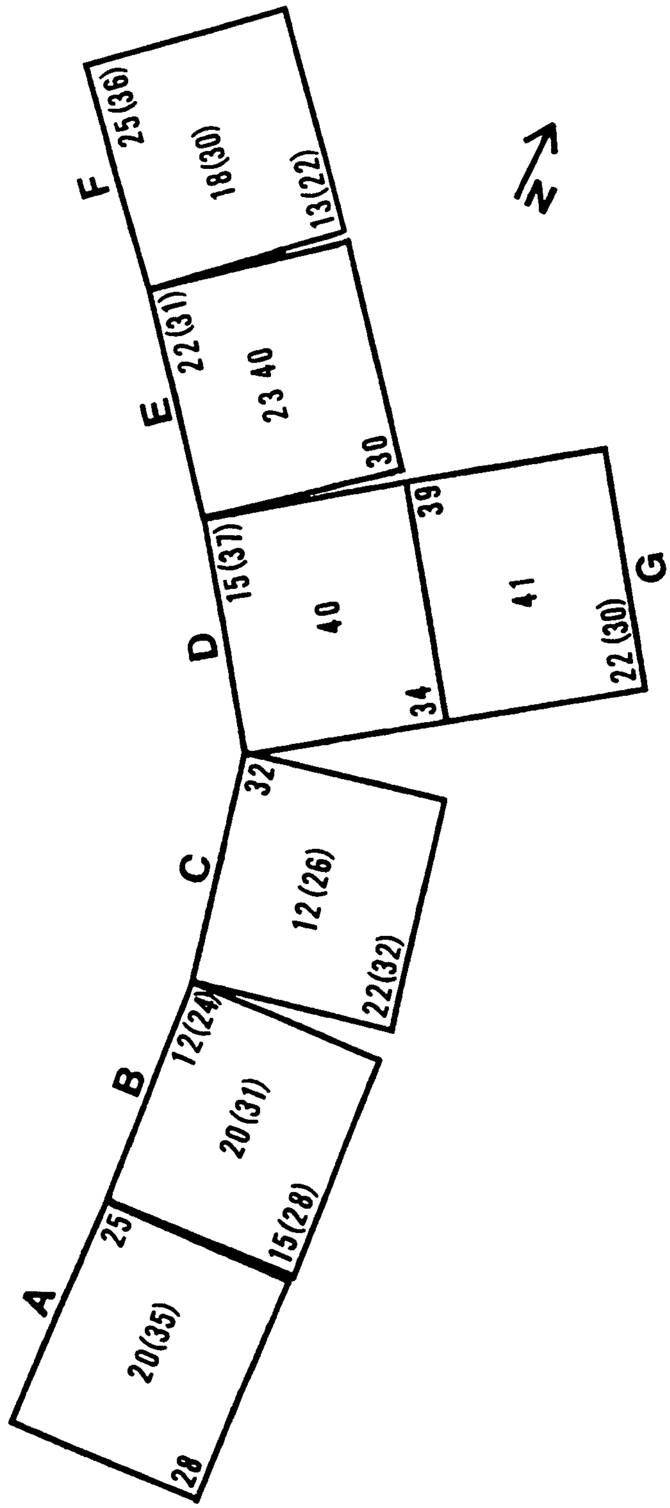
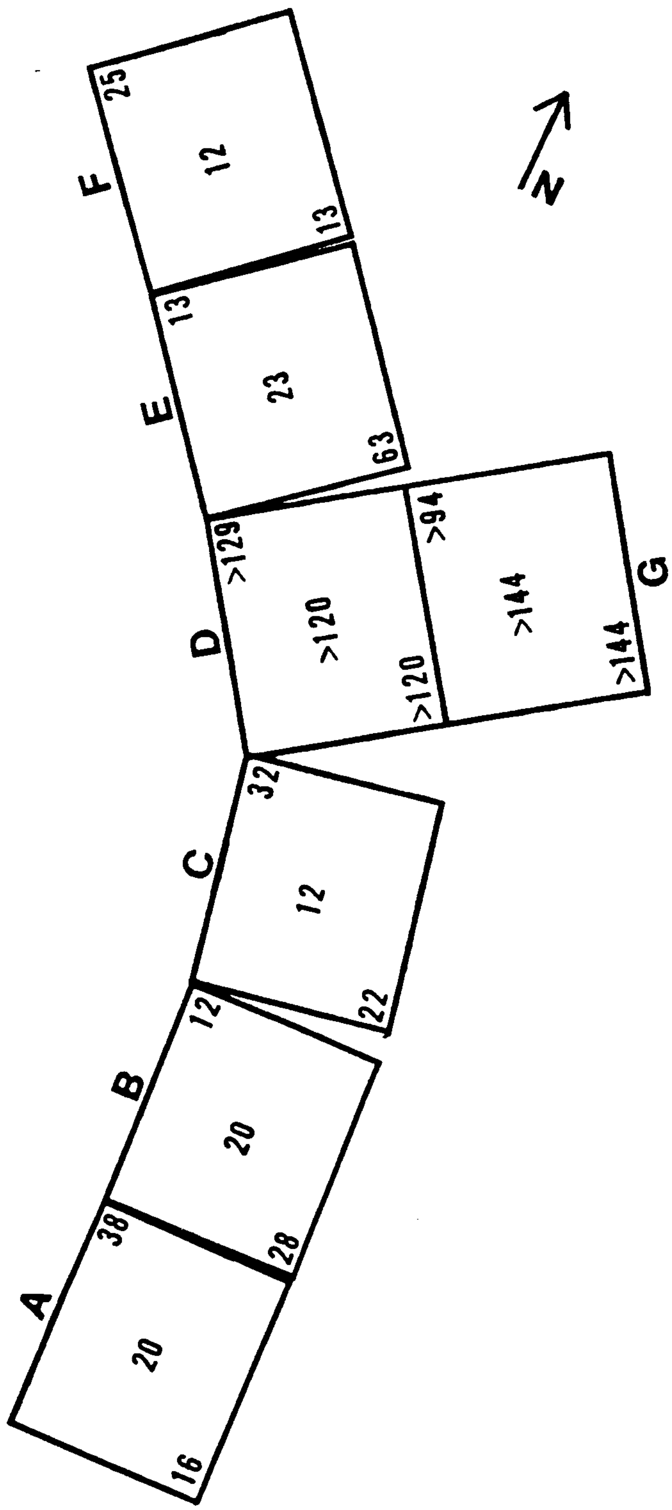

F
25(36)
18(30)
13(22)
E
22(31)
23 40
30
D
15(37)
40
34
39
41
22 (30)
G
C
32
12 (26)
22(32)
B
12(24)
20(31)
15(28)
A
25
20(35)
28

Figure B2. Topographic and soil conditions at experimental site:
3. Depth (cm) of carbonates in soil horizon (letters represent block designations)


N
F
25
12
13
E
13
23
63
D
>129
>120
>120
G
>94
>144
>144
C
32
12
22
B
12
20
28
A
38
20
16

APPENDIX C: SPECIES IN BLOOM AT TIME OF BURNS

18 May 1985
No data

29 June 1985
Amorpha canescens
Anemone spp.
Asclepias syriaca
Daucus carota
Erigeron annuus
Pastinaca sativa
Phleum pratense
Rosa spp.
Rudbeckia hirta
Sambucus canadensis
Stachys palustris
Verbena stricta

20 August 1985
Andropogon gerardii
Ambrosia spp.
Asclepias syriaca
Circium discolor
Daucus carota
Euphorbia corollata
Lactuca serriola
Lespedeza capatata
Monarda fistulosa
Solidago spp.
Sorghastrum nutans
Verbena stricta

6 May 1986
Fragaria virginiana
Lithospermum canescenes
Prunus americana
Taraxacum
Thlaspi arvense
Viola pedatifida

17 July 1986
Amorpha canescens
Andropogon gerardii--beginning
Agrimonia striata
Asclepias syriaca
Bouteloua curtipendula
Daucus carota
Desmodium illinoense
Echinacea pallida--finishing
Euphorbia corollata

17 July 1986 (continued)

Medicago lupulina
Melilotus alba
Monarda fistulosa
Pastinaca sativa--finishing
Petalostemum spp.
Rosa spp.--finishing
Sambucus canadensis
Stachys palustris
Verbena stricta
Veronicastrum virginicum

19 August 1986

Ambrosia spp.
Andropogon gerardii
Artemisia ludoviciana
Circium discolor
Daucus carota
Euphorbia corollata
Lactuca serriola--beginning
Lespedeza capatata
Monarda fistulosa
Oenothera biennis
Solidago spp.
Sorghastrum nutans
Trifolium pratense